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THE MARINE BORER FAMILY LIMNORIIDAE (CRUSTACEA, ISOPODA).

PART I: NORTHERN AND CENTRAL AMERICA: SYSTEMATICS, DISTRIBUTION, AND ECOLOGY[1,2]

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ABSTRACT

The family Limnoriidae is reestablished with keys and diagnoses to all known species including *Limnoria* (*Limnoria*) *lignorum* (Rathke), *L.* (*L.*) *pfefferi* Stebbing, *L.* (*L.*) *japonica* Richardson, *L.* (*L.*) *septima* Barnard, *L.* (*L.*) *quadripunctata* Holthuis, and *L.* (*L.*) *tripunctata* Menzies. The following are described as new species: *L.* (*L.*) *platycauda,* Dutch West Indies, *L.* (*L.*) *saseboensis,* Sasebo, Japan, *L.* (*L.*) *simulata,* Virgin Islands, *L.* (*L.*) *multipunctata,* Kai Islands, *L.* (*L.*) *unicornis,* Ponape Island, *L.* (*L.*) *foveolata,* Kai Islands, *L.* (*L.*) *sublittorale,* N. S. Wales, Australia, *L.* (*L.*) *insulae,* Fiji Islands. Seaweed borers were assigned to the new subgenus *Phycolimnoria,* containing *segnis* (Chilton), *antarctica* (Pfeffer) and the new species *algarum,* California, *segnoides,* Misaki, Japan, *nonsegnis,* Port Arthur, Tasmania, *rugosissima,* Port Jackson, Australia, and *stephenseni,* Auckland Islands. The new genus *Paralimnoria* was instituted to receive the tropical *L. andrewsi* Calman. Variations in salinity, temperature, dissolved oxygen, and food supply are considered the major factors influencing the distribution of the species. Literature citations are reasonably comprehensive.

INTRODUCTION

The object of this paper is to present a systematic and zoogeographic account of the wood and sea-weed boring marine isopods of the northern and central Americas. It is optimistically hoped that

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the introductory account of the morphology and the scientific keys are sufficiently elementary and lucid to permit a non-specialist to use them effectively.

The limnoria-like isopods which bore into wood are of such economic importance that they have been and are being studied by investigators of varied interest and training. It seems accordingly important that current systematic concepts and nomenclature be available and useful to the students of the subject.

The current concept suggests that only one species, *Limnoria lignorum* (Rathke) is widely present in the world. Other species which have been described have often been considered members of isolated endemic populations. This concept is apparently erroneous and thus highly misleading to students of the economic aspects, physiology, ecology, and geographic distribution of these animals. The evidence for the existence of other species, some of which seem to show even a wider distribution than *L. lignorum,* appears overwhelming to the writer and is here presented for a fairly wide geographic area.

In all, eight species are recorded from the area, including one apparently new genus, a new subgenus, and three new species. Five of the species had been known before, three from California alone.

Prior to the work of Richardson (1909, pp. 95-96, fig. 25) the characteristics used to distinguish the species were based mostly on the mouth parts, abdominal appendages, and the general body shape of the animals. While it is often true that features such as the shape of the maxillipedal epipod, and the number of articulations comprising the mandibular palp (both mouth parts) are useful in separating some species; these alone are insufficient to distinguish the many species now suspected to exist. In the course of this investigation it was found that the most useful diagnostic characteristics consisted of the gross and detailed shape and structure of ornamentations, tuberculations, and bristles on the dorsal surface of the last (most posterior) segment of the body, the *pleotelson.*

The following facts about the life habits of the animal are abundantly substantiated today. *Limnoria* and its close relatives (*Paralimnoria,* p. 147) eat the plant material, wood and seaweed, into which they bore. The habit of boring provides them with both nourishment and protection from enemies. The animals constitute a serious threat to wood, especially untreated wood, which is placed in sea water. They are exclusively marine and generally considered

inhabitants of shallow water but have been collected from depths as great as 290 fathoms. The methods which have been thus far devised of preventing their damage to wood, consisting usually of paints and injected preservatives, are still imperfect, and the problem of extending the life of treated wood is almost as acute today in some harbors as it was 50 years ago. Attack on wood is instituted by crawling or swimming adults and not by larval forms. The larvae are incubated in a brood pouch and carried by the adult until capable of doing their own boring. The released young, however, in contrast to the adults, are poor swimmers. Structurally, the animals, except for extensive modifications of the mandibles, are generalized isopods belonging to the least morphologically modified isopodan suborder, the Flabellifera.

Acknowledgments

The writer wishes first to thank the William F. Clapp Laboratories, Inc., of Duxbury, Massachusetts for their valuable assistance in supplying many of the specimens used in this study. The abbreviation "W.F.C.L." follows specimens which were received from that source. The encouragement of systematic studies by the late William F. Clapp was particularly stimulating to the writer. Surely his influence on marine borer studies will long be felt both here and abroad.

Numerous collecting trips were made to various harbors and bays in Southern California. On many of these excursions the companionship and collaboration with Dr. John Luther Mohr, Associate Professor of Zoology, University of Southern California, was both pleasant and intellectually rewarding.

Most of all the writer is indebted to the American Academy of Arts and Sciences for a grant-in-aid which permitted the procurement of essential literature and specimens from many parts of the world, as well as enabling the writer to participate in ecological studies of borers in San Francisco Harbor, Los Angeles Harbor, and other parts of California. In these studies, the use of laboratory and library facilities of the Pacific Marine Station, the Allan Hancock Foundation, and finally the Scripps Institution of Oceanography is especially appreciated as is also the assistance of the Office of Naval Research in supporting the terminal phase of this work.

Much of the descriptive material comes from a doctoral dissertation entitled "The phylogeny, systematics, distribution, and natural history

of *Limnoria*" which is deposited in the library of the University of Southern California, Los Angeles, California.

Review of the Literature

The literature dealing with *Limnoria* from North America may be conveniently divided into five major categories: taxonomy, distribution, ecology, anatomy, and physiology of the animals. It is the intent of this review to bring to the attention of the reader papers of outstanding importance to the general problem of each category rather than to discuss each paper.

Only one paper, that of Kofoid and Miller (1927) is of such scope as to cover all of the above subjects. It is based to a large extent on the findings of P.P.C. Hoek whose article "Betreffende de Levenswijze en de Werking van Limnoria lignorum" (1893) forms the starting point for much of our knowledge on the biology of the animal. A great deal of Hoek's work was both original and surprisingly accurate. The figures he gives of *Limnoria,* like those in the Kofoid and Miller paper (op. cit.), appear repeatedly in the works of later biologists concerned with the problem. Very recently Becker and Kampf, 1955, have reviewed the subject in a most comprehensive way.

Taxonomic Studies

Taxonomic studies on American *Limnoria* are most frequently found in treatises concerned with general isopodan systematics. The first to appear was that by Harger (1880), followed by Richardson (1905), and later by the Kofoid and Miller paper (op. cit.). The above papers mention only one species, *L. lignorum,* (Rathke), but in reality appear to treat several. Holthuis (1949) and Menzies (1951a) each added one species to the fauna, *L. quadripunctata* Holthuis and *L. tripunctata* Menzies. Without a doubt the most satisfactory taxonomic description of a species of *Limnoria* is that given by the venerable Norwegian scientist, George Ossian Sars (1897, pp. 76-77), and since he describes *L. lignorum,* a species which we consider, his study merits special note. The papers dealing with *Limnoria* on a world-wide scope are those by Chilton (1914a), Calman (1936), and Moll (1915). All of these suffer from the then prevalent concept that *L. lignorum* (Rathke) was the sole species having a world-wide distribution.

Distribution

With the exception of the papers by Richardson, Harger, and Kofoid and Miller, and some isolated reports by Holthuis (1949),

Menzies (1951a), and Menzies and Mohr (1952), no other papers are known which deal with the distribution of the *Limnoria* in the Americas. As far as the general distribution of the genus is concerned the papers (op. cit.) by Calman, Moll, and Chilton should be consulted. Chilton, Moll, Kofoid and Miller, and especially Omer-Cooper and Rawson (1934) all present some ideas on the methods utilized by *Limnoria* in obtaining its wide distribution.

Ecology

The papers of Johnson (1935) and Johnson and Miller (1935), dealing with the seasonal migration of *Limnoria lignorum* at Friday Harbor are the first American works on that subject. Johnson's is the first paper in which the phenomenon is critically examined. Seasonal settlement by that species was later studied in even greater detail by Sømme (1940) in Norway who further points out that the subject had been investigated by Kramp in Europe as early as 1927. Kofoid and Miller did not find a seasonal settlement by *Limnoria* in San Francisco Bay, but their results might now be questioned due to the finding that two species are present there, neither of which is *lignorum* (see pp. 158-162). Both species could have overlapping migratory periods which would mask one another. It is interesting to note that Greenfield (1952) was unable to pick out distinct seasonal or ecological preferences by *Limnoria* at Miami where at least three species are now known to occur (pp. 135, 137, 141). The papers by Henderson (1924) and Kofoid and Miller (1927) are the only ones in which the habits of *Limnoria* are treated in any detail. Shiino (1950) is one of the first investigators to provide a detailed analysis of a natural population. He was dealing with *Limnoria tripunctata* Menzies and *Paralimnoria andrewsi* (Calman), both of which species occur in North America. The parasites of *Limnoria* are briefly mentioned by Kofoid and Miller (1927). Important observations on development as it relates to distribution and seasonal behavior are given by Coker (1923) and Johnson and Menzies (1956) in America and Sømme (1940) in Norway. Reish (1954) lists and discusses the polychaetous predators of *Limnoria.*

Physiology

The papers dealing with the physiology of *Limnoria* are rather scarce. Those dealing with the salinity tolerances of the animal by White (1929), Coker (1923), and Kofoid and Miller (1929), present some striking differences as far as results are concerned.

Some of the differences are evidently due to variations in experimental methods used by those writers; others are probably due to the fact that they were all working with different species. In general it can be said that a salinity of 15‰ is surely lethal to the animals within a few days and that death ensues quite rapidly in lower salinities. The subject is in need of re-examination with more standard techniques in light of the evidence that different species exist.

The question of cellulose utilization by *Limnoria* was first experimentally examined by C. M. Yonge (1927) who reported negative results. This conclusion has since been questioned by Ray and Julian (1952) using a chemical method to detect enzyme activity. The investigators came to the conclusion that the animal was able to use cellulose and all express the doubt that the cellulase could have been elaborated by bacteria. ZoBell (1946) suggested that the sources of nitrogen for the animal might come from bacteria present in the burrows and gut of the wood borer. Adsorbed organic matter, pelogloea, the importance of which is discussed by Fox, Isaacs, and Corcoran (1952), might also constitute a primary source of nitrogen for *Limnoria*.

Anatomy

Studies of the anatomy of *Limnoria* are particularly scarce and those available deal largely with its external features. In North America Henderson's (1924) paper is one of the first attempts to understand the workings of the animal from its anatomical structure. Her account is comparable with the first European treatise on the subject by Coldstream (1836). Only the papers by Hoek and Miller and Kofoid (op. cit.) show any attempt at an understanding of the internal structures and in several details their reports are inaccurate. Accounts of specialized structures of *Limnoria* as compared with other animals have appeared in European journals most comprehensive of which is an account of the accessory organs of the brain by Amar (1951, p. 224). Menzies (1954) has described the reproductive system and certain aspects of the reproductive biology of *Limnoria*.

Economic Aspects of Limnoria Activity

No paper on marine wood-borers seems complete without an enumeration of the damages caused by the animals. There is, of course, no easy way to separate the damages caused by teredine borers from those caused by the isopods as far as cost alone is

concerned. Generally the two types of organisms work together in their destruction of wood in the sea. In a few instances where the salinity of the water is reduced to the point of exclusion of *Limnoria*, such as certain rivers near Sydney, Australia; Lake Maracaibo, Venezuela, and Mira Flores Lake, Panama, only the teredines cause the damages reported. With the advent of extensive pressure creosoting of marine piling, it seems that the damages of teredines have become much lessened in importance, whereas those of *Limnoria* have been increased. This appears due to the unusual ability of *Limnoria tripunctata* (Menzies, 1952) and perhaps other species, to enter the creosoted shell of treated wood shortly after its immersion in sea water. Teredine larvae seem unable to accomplish this feat until leaching or injury to the pile exposes virtually untreated surfaces. The fact that teredines penetrate wood as larval forms, whereas *Limnoria* penetrates the wood as an adult, would seem to have much to do with this difference in ability between the two to attack creosoted wood. It is generally known from the results of studies made on fouling organisms, that larval forms are frequently about 100 fold more sensitive to toxins than are the adults. As far as borers are concerned, this relationship is further augmented by reports of adult teredo penetrating the creosoted parts of piling after once gaining entrance through untreated areas.

The annual cost of marine borer damage in the coastal waters around the United States is believed to exceed 50 million dollars according to the most recent estimates available (Greathouse, 1952). In San Francisco Bay alone during the years 1917 to 1921, it was estimated that marine borers caused 25 million dollars damage. Recently the "premature" failure of piling in the Guantanamo Bay at a U.S. Navy Installation cost many thousand dollars (Alexis, 1951). Were the records available, these examples could be multiplied many times. Because much of the damage caused by borers is slow and unspectacular, it is only the sudden and dramatic failures of marine structures that find their way into the published records, and receive public attention. In Los Angeles Harbor the inspection and replacement of defective piling is a constant job and because of this very few major accidents due directly to borer damage, such as is shown in Figure 1, are recorded but it is the estimate of Mr. Carrol M. Wakeman, Chief Testing Engineer at the Los Angeles Harbor Department Testing Laboratory, that borers, mainly *Limnoria*, cause about one million dollars' damage each year.

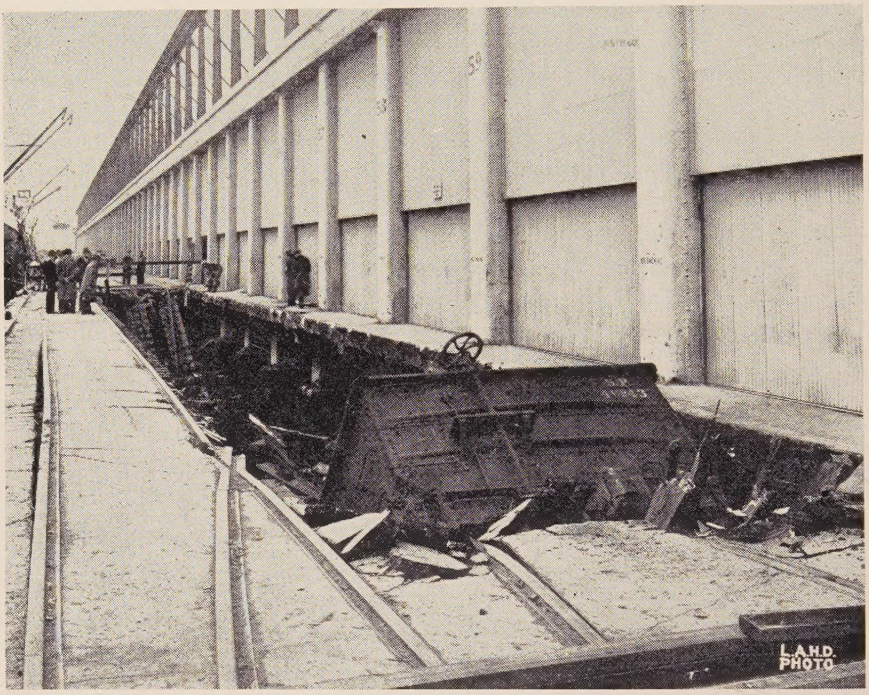

FIGURE 1. Collapse of creosoted wooden piles due to attack by *Limnoria tripunctata* at Berth 59, Los Angeles Harbor. Piles had been in service only 12-13 years. Photo courtesy of Los Angeles Harbor Department, via Mr. Carrol M. Wakeman, Testing Engineer.

COLLECTION, PRESERVATION AND EXAMINATION OF LIMNORIA FOR SYSTEMATIC STUDY

It is rather easy to detect the activities of the *Limnoria* which usually produce a multitude of minute holes at the surface of the wood. These holes are so numerous as to give the wood a lace-like appearance and a sponge-like structure. Attack on piling is often but not invariably most intense just above the mud line, giving the old piling the characteristic pencil-point appearance (Figure 2). The individual holes produced by *Limnoria* are seldom over one inch in length and generally penetrate less than one-half an inch into the wood. Usually the burrows are with the grain of the wood, the soft parts being more rapidly destroyed than the hard parts.

Not all samples of wood are equal in the number of animals they contain. Thus a sample taken from the soft and spongy outer part

generally has much fewer animals than one taken deeper in the wood (Figure 3). Many of the animals will be situated very near the blind end of their burrows. A sample of wood ¾ inches deep and about one inch square should yield a good supply of specimens, if the wood has animals at all.

The above remarks apply to the activities of the wood-boring *Limnoria*. Those that burrow into sea-weeds are much more difficult to detect and even more difficult to collect (Figures 3 and 4). These animals burrow into the holdfasts of kelps belonging to the Laminariales. They are often burrowing into the living tissue of the plant and are accordingly parasitic on the kelp. Plants with compact holdfasts, such as *Egregia, Laminaria,* and *Postelsia* are best examined for *Limnoria* by slicing thin sections off the exposed (outer) part of the holdfast. If *Limnoria* is present, its burrow will be cut through and be detected. It is then a matter of following one burrow until the animals, which are usually found in pairs, are discovered. Plants

FIGURE 2. Untreated Douglas fir piling in San Francisco Bay showing the pencil-point erosion of the piling, characteristic of *Limnorial* attack within the intertidal zone. Photo reproduced from Hill and Kofoid, 1927, fig. 13, with permission of the University of California Press.

FIGURE 3. Attack by *Limnoria*. (Top), on wooden piling (Douglas fir). (Bottom), on the hold-fast of the alga *Egregia*.

with a diffuse holdfast, such as *Macrocystis,* have long narrow "roots" (=rhizoids). In this case, one rhizoid frequently has only one burrow. This is most easily detected in the old part of the rhizoid and are not in newly formed tissue as in the case of *Egregia.* The older parts of the burrows are often inhabited by polychaets and small crustaceans; frequently they are filled with sand. It would seem that the attack of a holdfast by *Limnoria* would weaken its holding capacity, making it more liable to be detached from its moorings than an unattached plant. Suggestive of this is the fact that the large kelps which are cast upon the beach after a storm are often rich sources of specimens of the kelp-burrowing *Limnoria.*

Specimens preserved in 75 percent ethyl alcohol show a maximum number of identifying structures. In contrast, specimens preserved in formalin, a solution which is or often becomes acid, generally have lost much of their carbonate to the preservative with a resultant obscuring of the delicate sculpturing which is so very useful in making specific determinations.

The ornamentation of the pleotelson is best observed with the aid of a powerful binocular stereoscope and a concentrated reflected light of strong intensity. Specimens, especially if they are taken from turbid water, may be covered with a dense layer of debris. This debris,

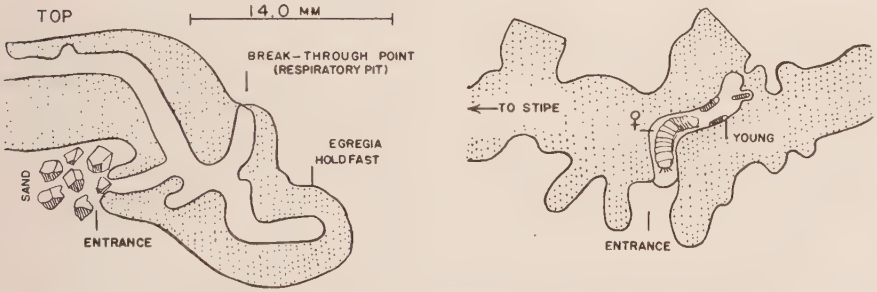

FIGURE 4. A sketch of the attack by *Limnoria* on the hold-fast of the seaweed *Egregia.*

consisting of silt, algal filaments, and wood particles must be removed from the pleotelson of the animal as it often obscures essential details in sculpturing.

For dissection of the mouth parts it is convenient to immerse the specimens in glycerin. The mouth parts can then be transferred to a microscope slide in the viscous drop of glycerin and readily examined.

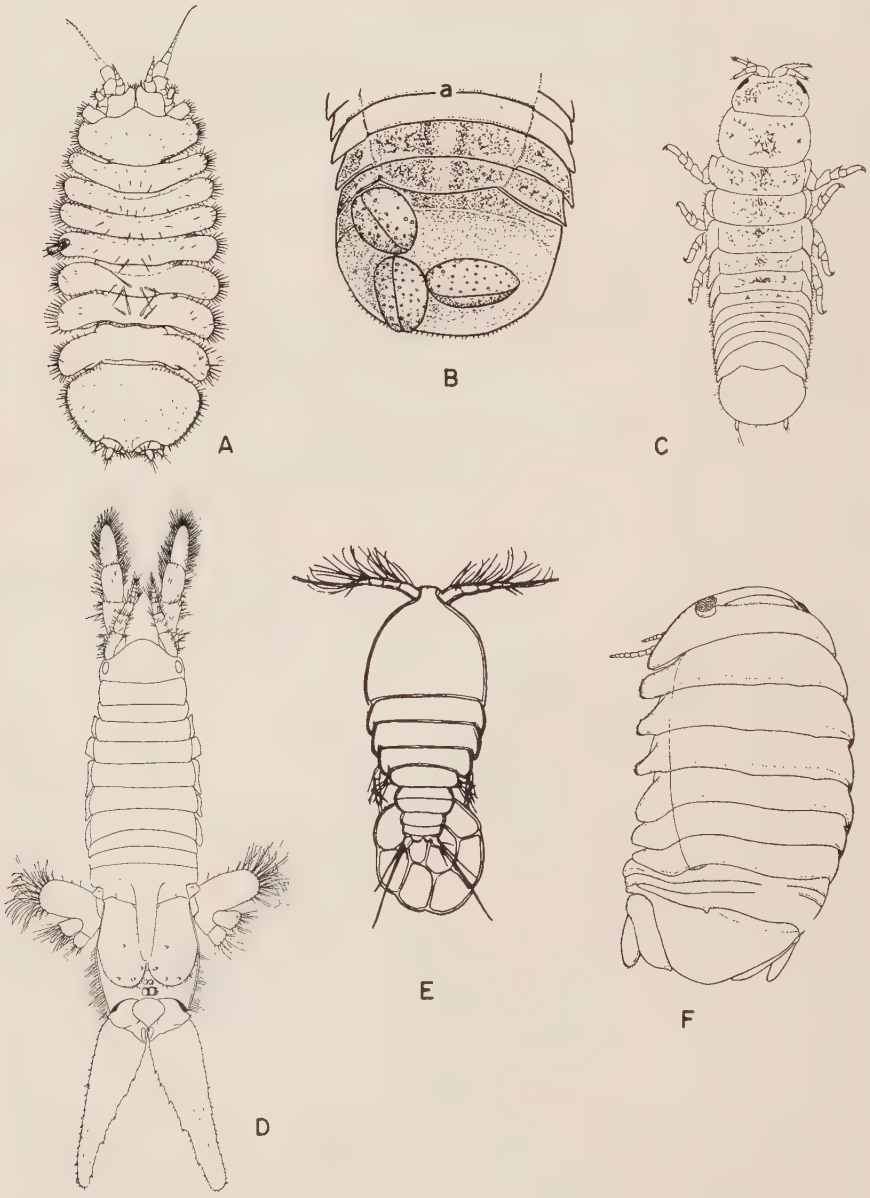

FIGURE 5. Crustaceans associated with *Limnoria* burrows. A, *Caecijaera* (after Menzies, 1951). B, *Aspidoconcha* (after DeVoss, 1953). C, *Limnoria* (after Shiino, 1950). D, *Chelura* (after Barnard, J. L., 1950). E, *Donsiella* (after Stephensen, 1935). F, *Gnorimosphaeroma* (after Menzies, 1954).

General Morphology

Recognition of *Limnoria* cannot always be based on the removal of specimens from holes in wood. At times the burrows are occupied by secondary invaders, such as the amphipod *Chelura,* isopods like *Sphaeroma,* or such commensals with *Limnoria* as *Caecijaera.* These associated animals are shown in Figure 5. The amphipod *Chelura* is so abundant at times that it often has been considered more dangerous than *Limnoria* and once was mistaken for *Limnoria* in an important article concerned with the prevention of damages by borers (Clavenad, 1879, pp. 73-144). As far as is now known, it appears that *Chelura* is of minor importance, being secondarily but invariably associated with *Limnoria* in nature. Species of the genus *Sphaeroma* which do little damage in the northern hemisphere seem to have caused extensive damage to wood in Australia (Iredale, Johnson, and McNeill, 1932, pp. 21-22).

Like all isopods, the body of *Limnoria* is divisible into three major regions, the cephalon or head, the peraeon or body (also thorax), and the posterior area, the pleon or abdomen (Figure 6).

The cephalon is recognizable as the globular area bearing the eyes and the following paired appendages, going from front to rear, first antennae, second antennae, mandibles, first maxillae, second maxillae, and those covering the mouth area externally, the maxillipeds.

The peraeon consists of seven ring-like segments (somites) each of which bears a pair of *peraeopods* (or legs). In the maturing and adult female each of the first four pair of peraeopods has a leaf-like extension at its inner (medial) base called an *oostegite.* Collectively the interleaving oostegites of the egg-bearing female (gravid female) form the brood pouch (also called marsupial pouch). Each peraeopod has seven articles. The elongate article nearest the animal's body is called the *basis*; those following are called successively the *ischium, merus, carpus, propodus,* and *dactyl.*

The terminal body area or peraeon consists of five small ring-like somites each of which bears a pair of leaf-like plates, the gills or *pleopods,* and a large semicircular plate-like segment, the *pleotelson* which laterally bears the *uropods.*

The amphipod *Chelura* may be distinguished easily from *Limnoria* by the fact that it has only three pairs of pleopods. The isopod *Sphaeroma* has only three segments to its abdomen and not six as does *Limnoria.* The isopod *Caecijaera* besides being blind and much smaller than *Limnoria* has only two segments comprising its abdomen.

Other associated organisms are so greatly different from *Limnoria* that a misinterpretation of them as the gribble seems unlikely.

Characters of Systematic Utility

Diagnostic characteristics, those relatively constant for each species, are found on several areas of the body.

The first antenna has a prominent scale (actually a rudimentary branch) in the genus *Paralimnoria,* (p. 147), which is either reduced

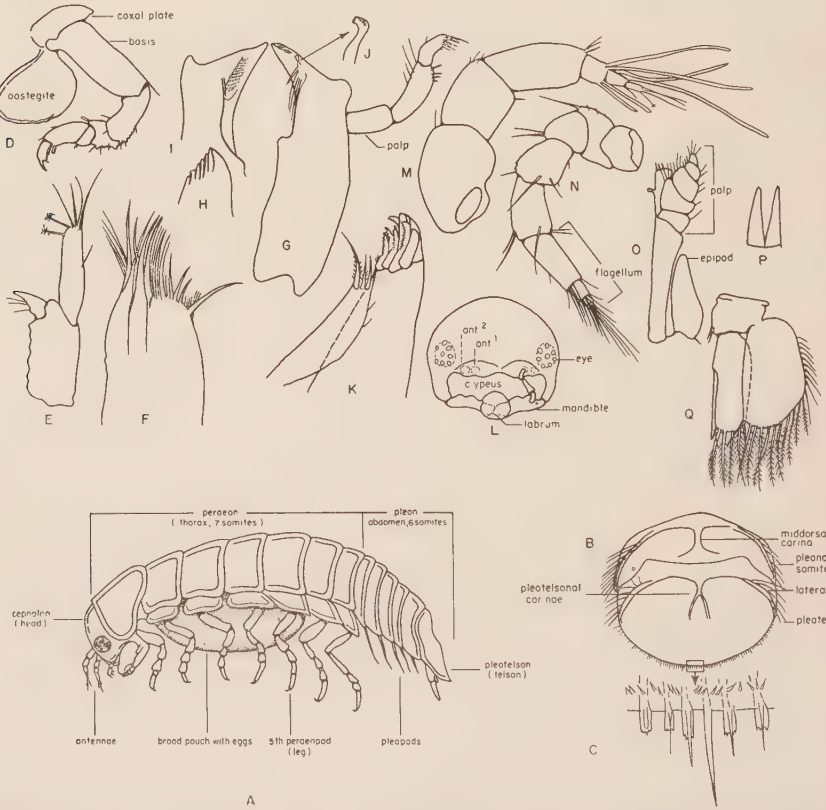

FIGURE 6. The external morphology of *Limnoria.* A, lateral view of gravid female (after G. O. Sars, 1897, and Menzies, 1954). B, Fifth pleonal somite and pleotelson. C, posterior border of pleotelson highly magnified. D, Leg of gravid female with attached oostegite. E, Uropod. F, First maxilla. G, right mandible of wood-borer. H, incisive part of right mandible of wood-borer, showing "file." I, Left mandible of wood-borer showing "rasp." J, Lacinioid seta of right mandible. K, Second maxilla. L, Frontal view of head. M, First antenna. N, Second antenna. O, Maxilliped. P, Penes (genital appophyses). Q, Second pleopod of male.

or absent in the genus *Limnoria* (sensu lato). The flagellum of the second antenna (Fig. 6) has four articles in some species (e.g. *L. (L.) pfefferi*) and five in others, (e.g. *L. (L.) lignorum*) or even six in *Paralimnoria*.

The mandible presents several important characteristics. The palp in all the species discussed herein has three articles (Fig. 6); whereas, in other species such as *L. (L.) segnis* Chilton (New Zealand) it has but two articles. The incisive process of each mandible bears a "rasp" and "file-like" series of grooves and teeth in the subgenus *Limnoria* (Fig. 6) and the genus *Paralimnoria*. These are lacking in the subgenus *Phycolimnoria*. The inner surface of the right mandible bears a lacinioid bristle or seta which is apparently distinctive for each species.

The epipod of the maxilliped (Fig. 6) has a shape and length peculiar to each species. In *L. (L.) lignorum* (Rathke) it does not quite reach to the articulation of the palp with the maxilliped; in other species it often extends farther.

The dorsal surface of the fifth somite of the pleon often has carinae (ridges) middorsally (*L. (L.) lignorum*) or elevated areas (*L. (L.) tripunctata*) or no ornamentation (*L. (L.) platycauda*) at all.

The dorsal surface of the pleotelson presents a multitude of useful characteristics. It can have rugosities (*L. (P.) algarum*) or be virtually smooth (*L. (L.) platycauda*). In some cases its margin has tuberculations (*L. (L.) tripunctata*) or no tuberculations, (*L. (L.) quadripunctata*). The setae or bristles fringing the posterior (distal) margin of the pleotelson are unique in their structure (microscopic) and arrangement. They consist only of simple closely set spike-like setae in *L. (P.) algarum* (p. 146), whereas they are delicate, often compound, and separated from one another in *L. (L.) tripunctata*. The lateral crests (Fig. 6) of the pleotelson have some characteristic tuberculations and setae.

In the species of the genus *Paralimnoria* the branches (*rami*) of the uropods are elongate and each taper to a point distally. On the other hand, the outer branch of the uropods (*exopod*) of *Limnoria* (sensu lato) is short and claw-like while the inner branch is elongated and not pointed, but blunt, at its apex.

Systematics

As is so often the case with animals of economic importance, *Limnoria* has had a varied history regarding its classification and relationships. When first formally described, it was included within

the genus *Cymothoa* (Rathke, 1799), a genus which today contains only fish parasites. In 1813 Leach described the genus *Limnoria*. This genus Leach placed in the family Cymothoidae of the tribe Asellides. According to Leach the tribe Asellides contained two additional families, the Anthuridae and Asellidae. The Cymothoidae then contained three genera, *Cymothoa, Limnoria* and *Sphaeroma,* each of which constitutes the type genus of a distinct family today. Subsequent to Leach (op. cit.), *Limnoria* has occupied a place in three other families. It was placed in the family Asellidae by White (1847, pp. 96-97) along with *Apseudes, Rhoea (=Tanais), Asellus, Jaera, Munna,* and *Oniscoda (=Janira).* Today *Apseudes* and *Tanais* are not considered isopods while the other genera belong to the suborder Asellota. A few years later White (1850, p. 68; 1857, p. 226) erected the family "Limnoriadae" for *Limnoria, Asellus, Jaera, Munna,* and *Janira.* Bate and Westwood (1868, p. 313) continued White's classification of the Asellidae in a peculiar and unusual way by recognizing the differences noticed by White, but by instituting a new name for the Apseudidae, e.g. the Tanaidae, and by disregarding the name "Limnoriadae"; however, remarking that Leach had earlier considered *Limnoria* to form a "separate class amongst his Cymothoades."

Harger (1880, pp. 371-373) was the first to consider *Limnoria* the type of a unique family, the Limnoriidae. He was, however, uncertain of this placement because he writes, "I have preferred to constitute a new family for the genus, which has, however, evident relations with the Sphaeromidae, and perhaps should yet be united with that family." This Gerstaecker (1881) does, and without mention of his system as new he places *Limnoria* in the Limnorina group of the family Sphaeromidae. Hansen (1905, p. 98) is more emphatic about the relationship and considers *Limnoria* as belonging to the subfamily Limnoriinae of the family Sphaeromidae.

Subsequent investigators seem to have followed Harger or Hansen without questioning the merits of either system.

Harger (1880, pp. 371-373) effectively demonstrated that *Limnoria* was much more like *Sphaeroma* than any of the Asellota. Curiously, neither Hansen nor Harger compared *Limnoria* with *Cirolana.* It appears that both were misled into believing *Sphaeroma* and *Limnoria* were related because both roll into a ball when disturbed. Actually they accomplish this feat with entirely different methods. In *Limnoria* the head slides under the anterior margin of the first peraeon-

TABLE 1.

COMPARISON OF GROUPS RELATED TO *Limnoria*

Characteristic	Cirolanidae *Cirolana*	Cymothoidae *Cymothoa*	Sphaeomidae *Sphaeroma*	Limnoriidae *Limnoria*
1. Head with dorsal occipital groove	Present	Absent	Present	Present
2. Eye location	Dorsal	Dorsal	Dorsal	Lateral
3. Clypeus	Two pieces	Single piece	Single piece	Single piece
4. First Antenna anterior (dorsal) to second	Yes	Yes	Yes	No (antennae on a line with each other)
5. Antennal scale in Adult	None	None	None	Present
6. First Maxilla	Bilobed	One lobe	Bilobed	Bilobed
7. Molar process of mandible	Compressed but large	Reduced	Large	Absent
8. Lacinia mobilis on mandible	Present	Present	Present	Absent
9. Setal row on mandible	Present	Absent	Present	Present
10. Maxilliped with epipod	Present	Absent	Absent	Present
11. Maxillipedal palp with	Five articles	Less than five articles	Five articles	Five articles
12. Coxal plates separate from body	Always	Always	Seldom	Always
13. Number of digestive caeca	Six	Six	Six	Four
14. Sexes	Separate	Protandric	Separate	Separate
15. Testis	Trilobed	Trilobed	Trilobed	Unilobed
16. Separate somites comprising the pleon	Six	Six	Three	Six

al somite; whereas in *Sphaeroma* the head overrides the first peraeonal somite. Furthermore, *Sphaeroma* bends mostly between the peraeon and pleon; whereas *Limnoria* bends on either side of the fourth peraeonal somite while enrolling.

In Table 1 is shown a comparison of major characteristics which illustrate the differences and similarities between the families Cirolanidae (as exemplified by *Cirolana*), the Cymothoidae (e.g. *Cymothoa*), the Sphaeromidae (e.g. *Sphaeroma*) and the genus *Limnoria*. The table indicates that *Limnoria* shares more characteristics (eight of those considered) in common with the Cirolanidae than with any of the other families. It does, however, show marked differences from the other families and accordingly it is suggested that the familial status of *Limnoria,* the Limnoriidae, be retained but without the reservation suggested by Harger.

Order ISOPODA
Suborder *FLABELLIFERA*
Family LIMNORIIDAE Harger, 1880, emended

Synonymy:

Limnoriidae Harger 1880, pp. 371-373. — Dahl, 1916, p. 28. — Pfeffer, 1887, p. 60.—Richardson, 1904, p. 8; 1905, p. 268.—Sars, G. O., 1897, pp. 75-76.—Shiino, 1950, p. 334.—Stebbing, 1905, p. 713.—Vanhöffen, 1914, p. 508.—Zirwas, 1911, p. 86.

Limnoriadae White, 1850, p. 68 (and synonyms); 1857, p. 226.

Asellidae (part), White, 1847, p. 96, 1857, pp. 225-227. — Bate and Westwood, 1868, pp. 349-350.

Sphaeromidae (part), Gerstaecker, 1881-1883, p. 220, *Limnorina* group.

Limnoriinae Hansen, 1905, p. 98 (see also pp. 75, 83, 92-94, 100, 115); 1916, p. 177.—O. Cooper and Rawson, 1934, pp. 28-30.

Diagnosis. Cephalon ovoid in cross section. Eyes lateral. Clypeus consisting of a narrow, transversely elongated, undivided piece, lacking projections in its outer surface. Antennae separated along mid-line; not contiguous at the base. First and second pairs of antennae nearly in a transverse line, neither one markedly more anterior than the other. Obvious scale present on first antennae. Mandible lacking lacinia mobilis and molar process. Posterior part of cephalon slips under anterior margin of first peraeonal somite. Sexes separate. Penis (genital appophyses) consisting of a pair of elongate plates which articulate with the body. Only four digestive caeca (glands) present. Testes each with one lobe. Coxal plates present on peraeonal somites two to seven. Uropodal branches tubular (or claw-like), not expanded and flattened. Maxilliped with an epipod and a pentarticulate palp. Pleon consisting of five somites plus a large semicircular pleotelson.

Composition. Previously the family was considered to have only one genus, *Limnoria*. This genus, however, may be conveniently split into

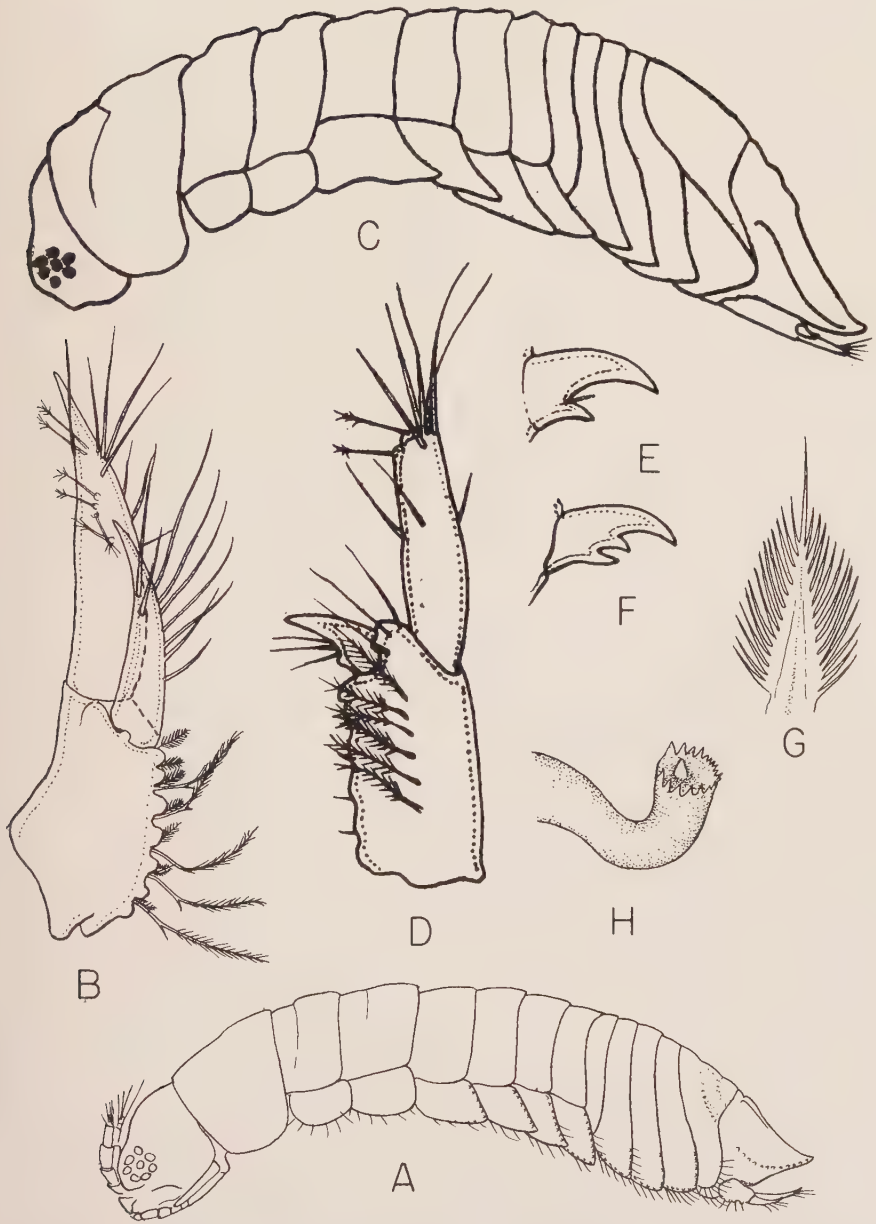

FIGURE 7. The distinguishing features of the genera of the Limnoriidae. A, *Paralimnoria,* lateral view. B, Uropod of *Paralimnoria.* C, *Limnoria,* lateral view. D, Uropod of *Limnoria.* E, Dactyl of first peraeopod of *Limnoria.* F, Dactyl of first peraeopod of *Paralimnoria.* G, Peculiar setae of peduncle of uropod of *Paralimnoria.* H, Lacinioid seta of mandible of *Paralimnoria.*

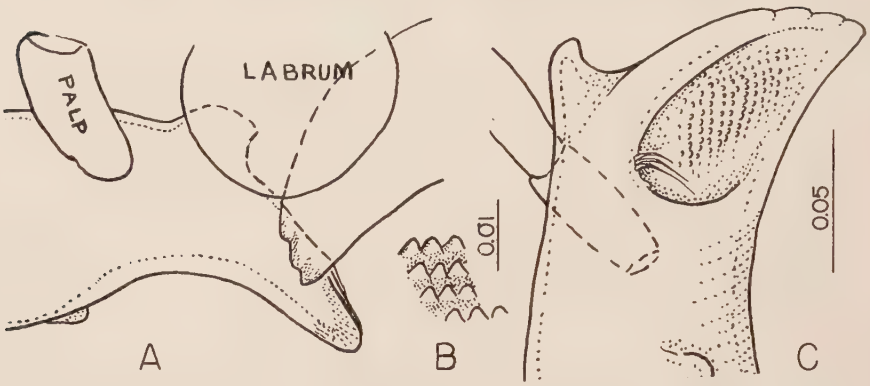

FIGURE 8. Mandibles of *Paralimnoria*. A, frontal view. B, "rasp" on inner surface of left mandible. C, inner surface of left mandible.

two genera, *Limnoria* Leach and a new genus *Paralimnoria,* which is herein described. The former genus may be further divided into two coordinate groups or subgenera; *Limnoria* (sensu stricto) containing only wood-boring species, and *Phycolimnoria* containing only algal-boring species. The distinguishing morphological characteristics between these divisions are shown in the following key and in Figures 7 and 8.

KEY TO THE GENERA AND SUBGENERA OF THE FAMILY LIMNORIIDAE

1. Branches of uropods dissimilar; exopod short, claw-like; endopod long and apically blunt. . . . . 2.
   Genus *LIMNORIA* (p. 121)

1. Branches of uropods similar; exopod and endopod elongate and each with an apical claw. . . . . .
   Genus *PARALIMNORIA* (p. 147)

2. Incisor of right mandible with file-like ridges on upper surface; that of left with a rasp-like arrangement of strongly sclerotized scales. . .
   Subgenus *LIMNORIA* (p. 122)

2. Incisors of mandibles simple, lacking "rasp" or "file." . . . . . .
   Subgenus *PHYCOLIMNORIA* (p. 144)

Characterization of Genera, Subgenera, and Species

The systematics of isopods is currently so unstable, as compared with other orders of the Crustacea such as the Decapoda, that even modern descriptions have been necessarily long. Accordingly, it is believed that a general statement of the method used here is needed.

In the descriptions which follow of genera and species, none of the characteristics already mentioned in the diagnosis of the family will be repeated. Descriptions of species will similarly be treated without repetition of generic characteristics. The diagnoses are kept as parallel as possible to facilitate comparisons.

Genus *Limnoria* Leach, 1813 (1814)

Synonymy:

Limnoria Leach, 1813, p. 433. — Bate and Westwood, 1868, p. 351.—Coldstream, 1836, pp. 316-334.—Harger, 1880, p. 373.—Hansen, 1905, pp. 98-100.—Hoek, 1893, pp. 1-97.—Nierstrasz, Schuurmans, and Stekhoven, 1930, p. Xe 79.—Richardson, 1905, pp. 269-270.—Sars, G. O., 1897, pp. 76-77.

Lemnoria Humphreys, 1845, p. 22.

Lunovia Fox, 1878, pp. 189-194.

Diagnosis. Flagellum of first antennae with four articles. Flagellum of second antenna with three, four or five articles. Mandibular incisor with or without "rasp" and "file." Lacinioid seta of right mandible always flattened, never tubular, and with apex of variable structure. Exopod of uropod much shorter than endopod and provided with an apical claw; endopod elongate, apex blunt, lacking claw. Fifth pair of pleopods lack marginal setae.

The list of synonyms given above is by no means a complete list of references to the genus by name. It is, on the other hand, a complete list of papers which characterize the genus, alter its characteristics, or presented different spellings of the name.

The first reasonably comprehensive diagnosis of the genus was given by Sars (1897, pp. 76-77). This was slightly altered by Hansen (1905, p. 100). Since then the concept has not changed. The diagnosis given here, except for emphasis on the characteristics which separate *Limnoria* (sensu lato) and *Paralimnoria* (p. 147), is very close to that given by Sars (op. cit.), Hansen, (op. cit.) and Richardson (1905, pp. 269-270).

Remarks. Previous writers attached no importance to the variation in the number of articles comprising the flagellum of the antennae. Harger (1880), in fact, was not certain it was multiarticulate. This characteristic is important in separating the genus *Paralimnoria* from *Limnoria* (sensu lato) and is useful further in characterizing various species of *Limnoria*.

The genus *Limnoria* contains two subgenera, *Limnoria* (sensu stricto) and *Phycolimnoria*. Examples of these are found in all the major oceans of the world, except in truly Arctic or Antarctic areas where wood or large sea-weeds are lacking.

Subgenus *Limnoria*, comb. nov.

Diagnosis. Members of the genus *Limnoria* (sensu lato) which have a "rasp" and "file" arrangement of scales and ridges on the incisive process of the mandibles. The species are all wood-borers.

Type species. *Limnoria (Limnoria) lignorum* (Rathke)

Besides having a "rasp" and "file" on the mandibles, the species of this subgenus differ ecologically from the members of *Phycolimnoria* in being able to burrow into wood. They are able to burrow into agar and presumably could burrow into kelp; however, they have not been found in kelps in nature. Most known species are inhabitants of the intertidal zone, but the record of *L. (L.) japonica* Richardson, collected from 163 fathoms from off Japan indicates that deep water species might be more abundant than has been generally believed. Seven species, including three new species, are considered in this paper. All currently known and valid species except *L. (L.) septima* Barnard, 1936, pp. 174-175, (Indian Ocean), and *L. (L.) japonica* Richardson, 1909, pp. 95-96 (Misaki Light, Japan) are described herein (see part II, p. 164.)

Key to the Northern and Central American Species of the Subgenus *Limnoria*.

1. Dorsal surface of distal border of pleotelson tuberculate (Fig. 16) . . . . . 2.
1. Dorsal surface of distal border of pleotelson smooth, not tuberculate (Fig. 10) . . . . . 4.
2. Flagellum of second antenna with four articles. Dorsal surface of pleotelson smooth with no elevated tubercles or ridges except at the tuberculate margin . . . . . *L. (L.) platycauda* (p. 139)
2. Flagellum of second antenna with five articles. Dorsal surface of pleotelson with elevated tubercles or carinae . . . . . 3.
3. Dorsal surface of proximal area of pleotelson, neither punctate nor rugose but with a single median tubercle followed distally by a pair of tubercles . . . . . *L. (L.) tripunctata* (p. 137)
3. Dorsal surface of proximal area of pleotelson punctate and rugose, with at least a pair of tubercles, one on either side of midline, each followed by a carina . . . . . *L. (L.) saseboensis* (p. 141)
4. Flagellum of second antenna with four articles. Pleotelson with two or no tubercles . . . . . 5.
4. Flagellum of second antenna with five articles. Pleotelson dorsally with four tubercles . . . . . *L. (L.) quadripunctata* (p. 127)

5. Epipod of maxilliped widest near distal end . *L. (L.) pfefferi* (p. 135)
5. Epipod of maxilliped widest near proximal end . . . . . 6.
6. Dorsal surface of pleotelson with λ-shaped carina on midline . . . . . *L. (L.) lignorum* (p. 123)
6. Dorsal surface of pleotelson medially with a pair of tubercles . . . . . *L. (L.) simulata* (p. 144)

Limnoria (Limnoria) lignorum (Rathke)

Figure 9

Synonymy:

Cymothoa lignorum etc., Rathke, 1799, pp. 101-104, pl. III, figs. 14a-14d.

Limnoria terebrans Leach, 1813, p. 433.

Limnoria lignorum (Rathke), White, A., 1857, pp. 227-230. pl. XII, figs. 5.—Black and Elsey, 1948, pp. 1-29.—Calman, 1898, p. 261.—Fee, 1926, pp. 27-28.—Fraser, 1923, pp. 159-167.—Guberlet, 1936, p. 337, photograph, p. 336.—Hatch, 1947, pp. 211-212, fig. 81 (part).—Henderson, 1924, pp. 1-17.—Johnson, 1935, pp. 427-438, tab. 1-4.—Johnson and Miller, 1935, pp. 10-12, 17.—M'Gonigle, 1925, pp. 1-67.—Stafford, 1912, pp. 52, 60.—White, F. D., 1929, pp. 9-18.

Limnoria tenebrans Leach, Richardson, 1905, p. 269 (in part, a misspelling of *terebrans*).

Diagnosis. Scale of first antenna evident. Flagellum of second antenna with four articles. Epipod of maxilliped triangulate, about two and three-quarters times as long as wide, not quite reaching the articulation between palp and endopod. Mandibular palp with three articles. Fifth somite of pleon with a mid-dorsal longitudinal carina. Pleotelson with an anteriorly situated mid-dorsal longitudinal carina which bifurcates posteriorly and lacks tubercles. Posterior margin of telson lacks tubercles but has a dorsal fringe of spike-like bristles. Lateral crests of pleotelson slightly tuberculate. Lacinioid seta of right mandible with apex complex, trifid, and abruptly bent.

Type locality. Norway, probably Bergen (Rathke, 1799). Type specimens are not known to exist.

Measurements. The size of this species varies considerably. It is one of the largest of the wood-boring species, especially in the northern and colder regions of its range. A female of average size from Kodiak, Alaska was 3.5 mm in length and 0.8 mm in pleotelsonic width.

Remarks. The original description of *Cymothoa lignorum* by Rathke (1799, pp. 101-104, pl. III, figs. 14a-14d) presents one important nomenclatural problem. The description *per se* is polynomial and not binomial. The figure (part of the description in the broad sense) is given a binomial label. Subsequent writers have wisely considered, therefore, that Rathke satisfied the requirements of the Linnaean system of nomenclature. Linnaeus appears to have been unaware of *Limnoria,* but it is interesting to note, as Dahl (1916, p. 29) points

FIGURE 9. *Limnoria (L.) lignorum* (Rathke), topotypic male. A, distal parts of uropods. B, distal article of first antenna. C, apex of pleotelson. D, lacinioid seta of right mandible. E, maxilliped. F, pleotelson. G, distal parts of first peraeopod. H, lateral crest of pleotelson. I, flagellum of second antenna. Figures with similar magnification, A, E; B, G, H, I; C-, D-, F.

out, that Linnaeus' (Syst. Nat. ed. 10, 1758, p. 637) description of *Oniscus marinus* "semicylindricus, cauda ovato-oblonga integra," applies better to *Limnoria lignorum* (Rathke) than to the species known today by the name *Jaera marina* (Linne). Dahl (op. cit.) seems reasonably certain that Linnaeus had seen neither *L. lignorum* nor *J. marina* but, perhaps, a species of *Idothea*.

That the species *Cymothoa lignorum* Rathke belonged to the genus *Limnoria* Leach was recognized by White (1857, pp. 227-230, pl. XII, fig. 5) who considered Leach's species *L. terebrans* a synonym of Rathke's *lignorum*. Unfortunately, several writers subsequently cited the species as *"Limnoria lignorum* White" in an apparent attempt to credit White with the new combination. Actually such a citation means that White and not Rathke described the species which is, of course, not the case.

Through the courtesy of Dr. Isabella Gordon of the British Museum (Natural History), I was able to examine seven specimens (cotypes) of Leach's *Limnoria terebrans* collected from the Bell Rock lighthouse, Scotland, by Robert Stevensen in 1807. These specimens have been compared with over 200 specimens of *Limnoria (L.) lignorum* (Rathke) from Trφmso, Kristiansund, Flφdvigen, Rong, and Klosterelu Fjord in Norway and appear identical with Leach's specimens. White's (op. cit.) union of *terebrans* with *lignorum* accordingly is substantiated. This is a matter of considerable taxonomic importance in view of Holthuis' (1949, pp. 167-172) discovery of *Limnoria (L.) quadripunctata* in Holland where, however, *Limnoria (L.) lignorum* appears to be the common and indigenous species.

The figures and description given this species by Sars (1897, pp. 76-77, pl. 31) are outstanding and have been reproduced freely by subsequent investigators, including myself (Fig. 6A). Unfortunately Sars failed to notice the carinae on the dorsal surface of the pleotelson and the distinctive number of articles of the antennal flagellum, but beyond that he omitted few details. There is no real utility in enumerating errors in the descriptions and figures given by Leach and Rathke except to point out that both investigators figured the body of the animal as having more somites (segments) than it actually has. Detailed structures were even less accurately delineated.

Material examined. Including those mentioned above from Europe,

the following specimens were examined from localities in North America:

Atlantic Coast

Newfoundland. *Argentia,* April 1, 1949, 6 specimens, W.F.C.L.

Nova Scotia. *Liverpool,* April 1, 1948, 8 specimens, December 1, 1949, 20 specimens, W.F.C.L.

Maine. *Casco Bay,* 1873, 9 specimens, U. S. Fish Commission, U.S.N.M. Cat. No. 2254. *Wicasset,* 1949, 7 specimens, W.F.C.L. *Fort Preble,* March 1949, 6 specimens, W.F.C.L. *Rockland,* 5 samples, 1948-1950, 47 specimens, W.F.C.L. *Portland,* 7 samples, 1949-1950, 76 specimens, W.F.C.L. *Southwest Harbor,* 5 samples, 1948-1950, 51 specimens, W.F.C.L.

New Hampshire. *Portsmouth,* 7 samples, 1948-1950, 59 specimens, W.F.C.L.

Massachusetts. *Boston,* 17 samples, 1948-1950, 174 specimens, W.F.C.L. *Quincy,* 2 samples, 1948, 1950, 12 specimens, W.F.C.L. *Salem,* 2 samples, 1948, 28 specimens, W.F.C.L. *Charleston,* 2 samples, 1948, 21 specimens, W.F.C.L. *Port Alleston,* January 1, 1950, 20 specimens, W.F.C.L. *Gloucester,* December 9, 1948, 5 specimens, W.F.C.L.

Rhode Island. *Newport,* April 8, 1949, 5 specimens, W.F.C.L.

Pacific Coast

Komandorski Islands, Bering Island, N. Grebnitski, no date, 75 specimens, U.S.N.M. Cat. No. 13081.

Alaska. *Adak,* 2 samples, 1948, 1950, 11 specimens, W.F.C.L.; 1950, 2 specimens, Charles H. Edmondson. *Dutch Harbor,* December 5, 1949, 9 specimens, W.F.C.L. *Kodiak,* February 16, 1949, 4 specimens, W.F.C.L.; 10 specimens, Charles H. Edmondson (date?). *Sitka,* March 9, 1949, 7 specimens, W.F.C.L.

British Columbia. *Victoria,* Departure Bay, Vancouver Isl., 1912, 1 specimen, Miss Pixell, British Museum (Natural History).

Washington. *Bellingham,* 2 samples, 1950, 12 specimens, W.F.C.L. *Hadlock,* March 18, 1949, 8 specimens, W.F.C.L. *Port Angeles,* 2 samples, 1949, 19 specimens, W.F.C.L. *Port Townsend,* 3 samples, 1948, 1950, 24 specimens, W.F.C.L. *Neah Bay,* 2 samples, 1949-1950, 22 specimens, W.F.C.L. *Friday Harbor,* 1949, 25 specimens, Dr. John L. Mohr. *Seattle,* December 6, 1948, 7 specimens, W.F.C.L.

Oregon. *Coos Bay,* Coos Co., August 1950, 23 specimens, Donald J. Reish.

California. *Samoa,* April 11, 1949, 2 specimens (with *L. (L.) quadripunctata*), W.F.C.L. *Point Arena,* 4 samples, 1948-1949, 40 specimens, W.F.C.L.

Geographical distribution. On the Pacific Coast the species extends from about 58°N (Kodiak Isl., Alaska) to 39°N (Point Arena, California). On the Atlantic Coast the distribution, as now known, appears restricted between 47°N (Argentia, Newfoundland) and 42°N (Rhode Island). Presumably it will be found farther north on the Atlantic side when more samples are available. It has been reported by Stephensen (1929) from Western Iceland (ca 63°N).

Factors associated with the distribution are discussed on p. 158.

Limnoria (Limnoria) quadripunctata Holthuis

Figures 10-14

Synonymy:

Limnoria quadripunctata Holthuis, 1949, pp. 167-172, fig. 2. — Menzies and Mohr, 1952, pp. 81-86.

Limnoria lignorum (Rathke). — Kofoid and Miller, 1927, p. 208, fig. 124 (not the remainder of the references and figures which might apply to other species).—MacGinitie, 1935, p. 703.—Schmitt, 1931, p. 217, fig. 41 (only this figure).

Diagnosis. Flagellum of second antenna with five articles. Epipod of maxilliped triangulate, not quite reaching the articulation between the palp and the endopod. Mandibular palp with three articles. Fifth somite of pleon dorsally with an x-shaped carina on mid-line. Pleotelson anteriorly with a pair of tubercles on mid-line followed by a similar pair of short distance from anterior pair. Each tubercle of posterior pair is followed by an indistinct longitudinal carina (especially evident in female specimens). Posterior margin of pleotelson dorsally lacks tubercles, spike-like bristles evident. Lateral crests of pleotelson lack tubercles. Lacinioid seta of right mandible expanded at apex which bears a fringe of serrations.

Type locality. North Sea coast of the Dutch province of Zuid-Holland between the villages of Katwijk and Noordwijk, not far from Leiden. October 24, 1948, S. Kroonenberg and L. B. Holthuis, more than 100 specimens (Holthuis, 1949, p. 172). The types are located in Rijksmuseum van Natuurlijke, Leiden.

Measurements. Length 3.0 mm; width 1 mm; (Holthuis, 1949, p. 167). Large female, length 3.4 mm, pleotelsonic width 1.0 mm.

Remarks. Holthuis' (1949) description is particularly good; however, a few points need elaboration and correction. The median carina of the fifth somite of the pleon is forked at both the anterior and posterior ends and not only at the anterior end. The eyes each have seven paired ocelli. The flagellum of the first antenna consists of five

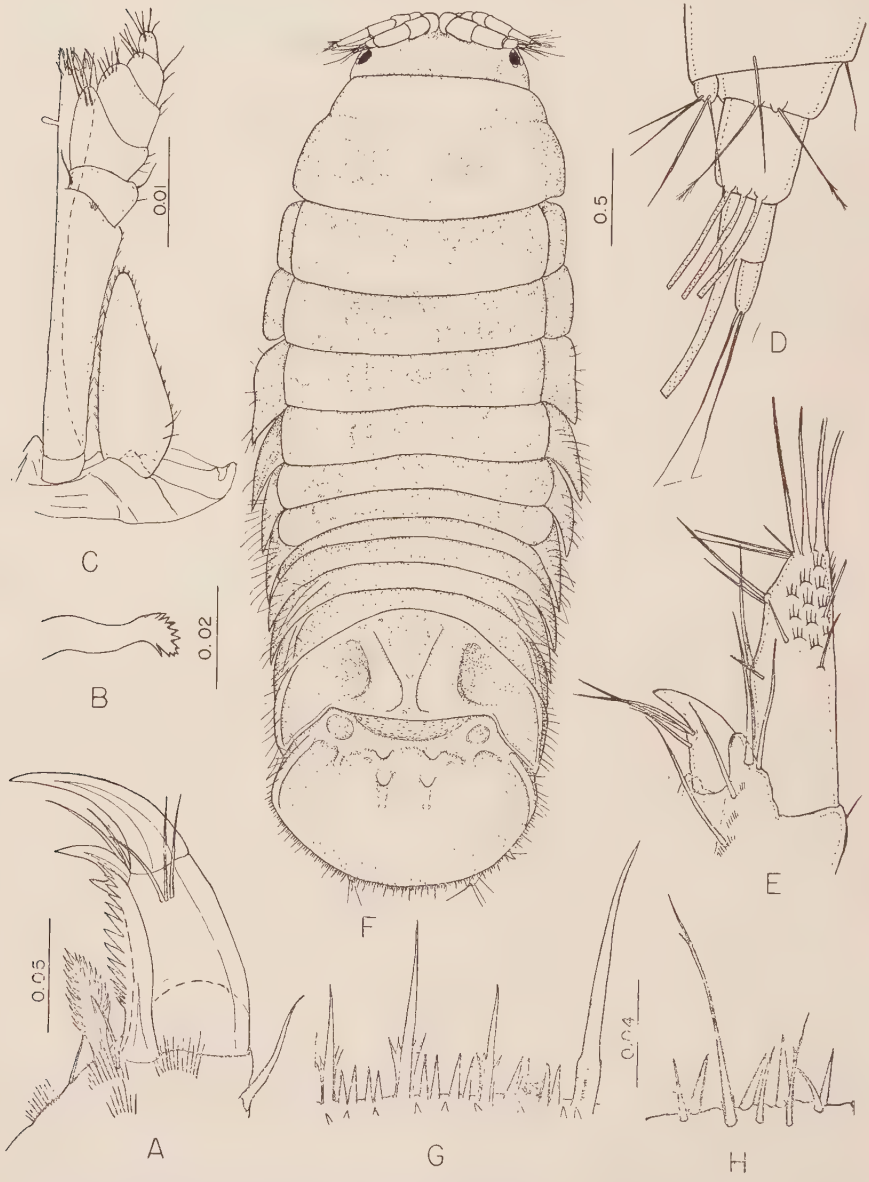

FIGURE 10. *Limnoria (L.) quadripunctata* Holthuis. A, distal part of first peraeopod. B, lacinioid seta of right mandible. C, maxilliped. D, distal articles of first antenna, note antennal scale. E, uropod. F, female, dorsal views, homoeotype. G, posterior edge of pleotelson. H, lateral crest of pleotelson. Figures with similar magnification, A, D, G, H; B; C; E; F.

FIGURE 11. *Limnoria (L.) quadripunctata* Holthuis, mouth parts. A, labium, right. B, left mandible, inner surface. C, apices of left and right mandible *in situ,* showing functional relationship. D, setal row of left mandible. E, coupling hook. F, second maxilla. G, apex of endopod of maxilliped. H, upper (cutting surface) of incisive process of right mandible showing "file." I, peculiar setae at apex of endopod of maxilliped. J, inner surface, left mandible showing "rasp." K, lacinioid seta of right mandible. L, first maxilla. Figures with similar magnification, A, B, K, J; C, F, G, H, L; D, E, I, K.

FIGURE 12. *Limnoria (L.) quadripunctata* Holthuis. A, uropod, juvenile, 1.0 mm length. B, first antenna. C, setal row of left mandible. D, second antenna. E, uropod. F, genital apophyses. G, eye, lateral view. Figures with similar magnification, A; B, D, E, F; C; G.

FIGURE 13. *Limnoria (L.) quadripunctata* Holthuis, peraeopods; A-G, in order, the first to seventh pair of adult. H, sixth of juvenile of 0.9 mm length. I, first of juvenile 0.9 mm in length. J, merus, outer surface, first peraeopod, adult. Figures with similar magnification, A-G; H-J.

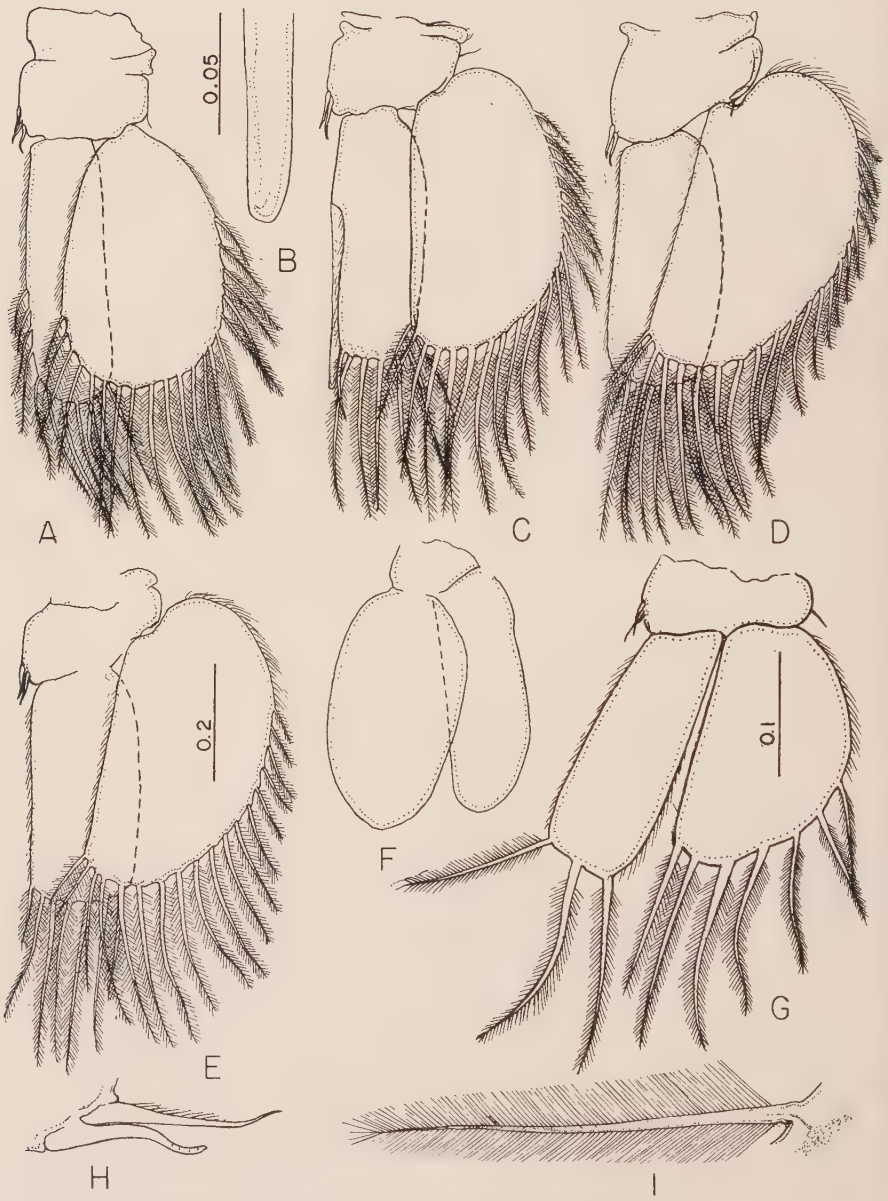

FIGURE 14. *Limnoria (L.) quadripunctata* Holthuis, pleopods. A-F, first to fifth of adult male. G, first, juvenile 0.9 mm length. H, accessory setae of sympod. I, plumose seta of pleopod. Figures with similar magnification, A, C, D, E, F; B, H, I; G.

articles and is thus unlike the quadriarticulate flagellum of *L. (L.) lignorum*. The maxillipedal epipod (Holthuis, 1949, p. 168, fig, 2e) is neither as short as figured nor is it shorter than that of *L. (L.) lignorum*. Each maxilliped has one coupling hook. The exopod of the uropod is not distinctly smaller than that of *L. (L.) lignorum*, but actually the two are very similar. The uropod is not similar to that of *L. (L.) septima* Barnard whose peduncle is markedly more elongate than that of *L. (L.) quadripunctata.*

Kofoid and Miller (1927, fig. 124) show, as Holthuis (op. cit.) pointed out, a clear series of photographs of *L. (L.) quadripunctata.*

Material examined. Including 15 specimens of Holthuis' type series, the following have been examined from the area under consideration:

Pacific Coast

California. *Samoa,* Humboldt Co., March 11, 1949, 10 specimens (with *L. (L.) lignorum*) W.F.C.L. *Bodega Harbor,* February and March, 1949, 61 specimens, R. J. Menzies and L. Miles. *Tomales Bay,* Nick's Cove, Vilich's Pier, Hamlet and Inverness, 1947-1949, 112 specimens, R. J. Menzies. *Duxbury,* April 12, 1949, 15 specimens, R. J. Menzies. *San Francisco Bay,* 1949-1950, several hundred specimens from Yerba Buena Isl., Belvidere, Parr-Richmond Pier, Aquatic Park, India Basin, Hunter's Point, Tiburon, N.W. Pac. R.R. ferry landing, Sausalito, Richmond at ferry landing, W.F.C.L., and Mr. R. J. Menzies and Mrs. Betty G. Menzies; Berkeley yacht harbor, September 8, 1950, 4 specimens, Dr. J. L. Mohr. *Monterey Bay,* 1949-1950, 59 specimens, W.F.C.L., July 22, 1947, 4 specimens, E. Polhemus and L. Kellen. *Elkhorn Slough,* July 1949, 5 specimens, R. J. Menzies. *Morro Bay,* 7 samples, 1949-1950, hundreds of specimens, R. J. Menzies and Dr. J. L. Mohr. *Santa Barbara,* 1949, 6 specimens, W.F.C.L. *Point Hueneme,* 1949, 14 specimens, W.F.C.L. *Los Angeles-Long Beach Harbors,* 1949-1950, hundreds of specimens, Southern California Marine Borer Council. *La Jolla,* August 24, 1949, 20 specimens, R. J. Menzies.

Geographical distribution. The species is noteworthy for its apparent absence from the Atlantic coast and from its restricted distribution between 41°N (Samoa, California) and 33°N (La Jolla, California). This corresponds roughly to areas having a mean annual sea water temperature (surface) near 15°C (10-20°C). In San Francisco Bay and south of Morro Bay the species appears restricted to the colder harbor entrances and does not penetrate into the warmer areas. It was the only species found at Tomales Bay.

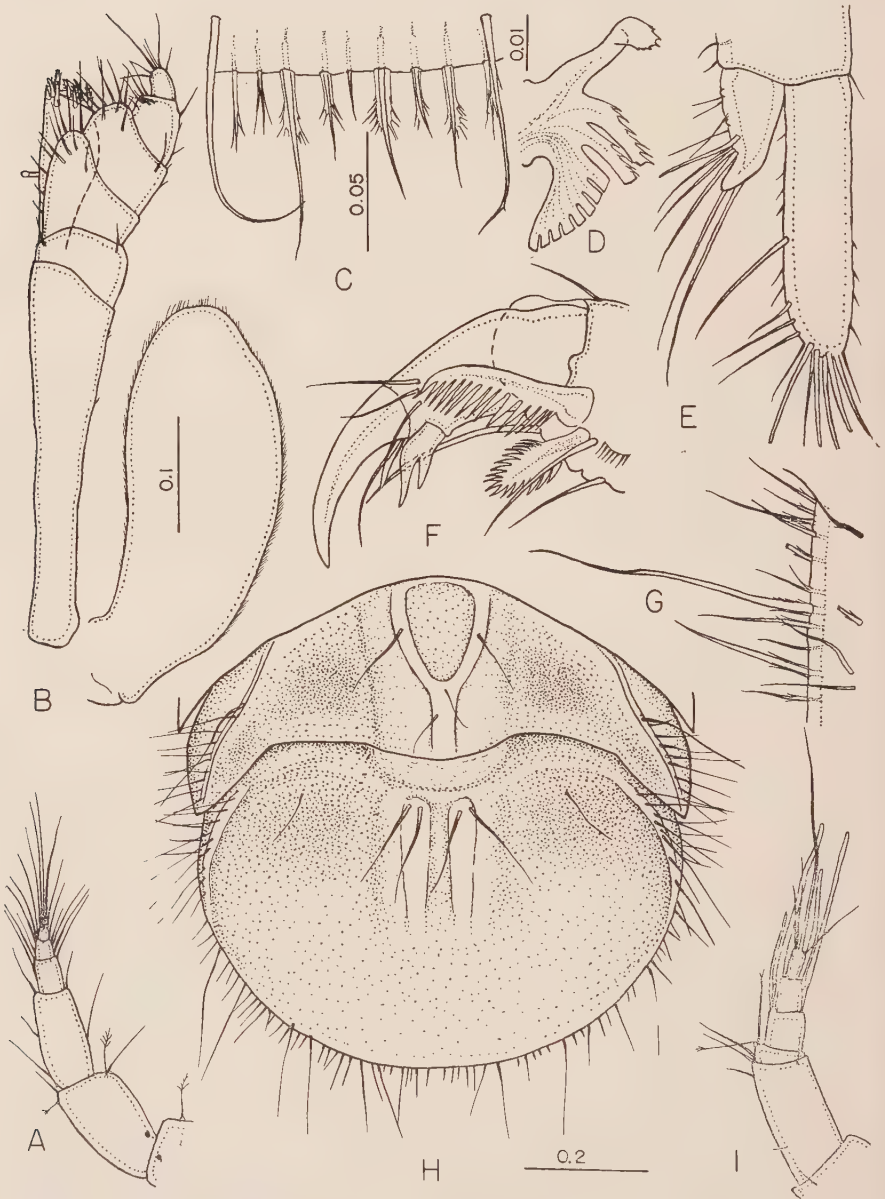

FIGURE 15. *Limnoria (L.) pfefferi* Stebbing, female cotype. A, second antenna. B, maxilliped. C, posterior edge of pleotelson. D, setal row and lacinioid seta of right mandible. E, uropod, distal parts. F, first peraeopod, distal parts. G, lateral crest of pleotelson. H, pleotelson, dorsal view. I, first antenna. Figures with similar magnification, A, B, E, F, I; C, G; H; D.

Limnoria (Limnoria) pfefferi Stebbing

Figure 15

Synonymy:

Limnoria pfefferi Stebbing, 1905, pp. 714-715. pl. LIIIa. — Chilton, 1914a, pp. 382, 387.—Kofoid and Miller, 1927, p. 309. —Holthuis, 1949, p. 170.—Moll, 1915, pp. 184-185, 188, fig. 7. *non Limnoria* (*pfefferi* Stebbing?), Stephensen, 1927, pp. 361-362 (=*Limnoria (Phycolimnoria)* sp).

Diagnosis. Flagellum of second antenna with four articles. Epipod of maxilliped just reaching the articulation of the first article of the palp with endopod; epipod clavate, widest near distal end, about two and one-half times as long as wide. Mandibular palp with three articles. Fifth somite of pleon dorsally with a median longitudinal yoke-shaped carina. Dorsal surface of posterior edge pleotelson lacks tubercles and spike-like bristles; lateral crests devoid of tubercles. Lacinioid seta of right mandible short, with five apical denticles.

Type locality. Minikoi Atoll, Indian Ocean, in rotten wood in lagoon (Stebbing, 1905, p. 715). The types are located in the British Museum (Natural History).

Measurements. Stebbing (1905, p. 715) records the species as being 3.5 mm in length and 1.25 mm in breadth. A large female cotype examined by me was 3.4 mm long and had a maximal pleotelsonic width of 0.75 mm.

Remarks. Stebbing (op. cit.) appears to have had two species at his disposal when describing *pfefferi.* The uropods figured by Stebbing belong to a species of *Paralimnoria* (p. 147) and not *Limnoria* (sensu lato). In other general features Stebbing's description applies to the cotypes (one male and one female) which are here figured and which kindly were sent to me for examination by Dr. Isabella Gordon of the British Museum (Natural History). Stebbing apparently failed to notice the conspicuous and characteristic carinae of the fifth somite of the pleon and pleotelson because he calls the area of the pleotelson on which the parallel ridges are present a "smoothly rounded median elevation."

The specimens from the Auckland Islands which Stephensen (1927, pp. 361-362) doubtfully assigned to as *pfefferi* have been examined and referred to the sea-weed borer, *L. (P.) sp.* (see part II).

Material examined. Besides the cotypes of this species, two males and one female were examined from the county causeway, Miami Beach, Florida. These were collected on September 1, 1950 by Mr. Leonard Greenfield of the University of Miami Marine Laboratory.

Geographical distribution. The species, besides having been first

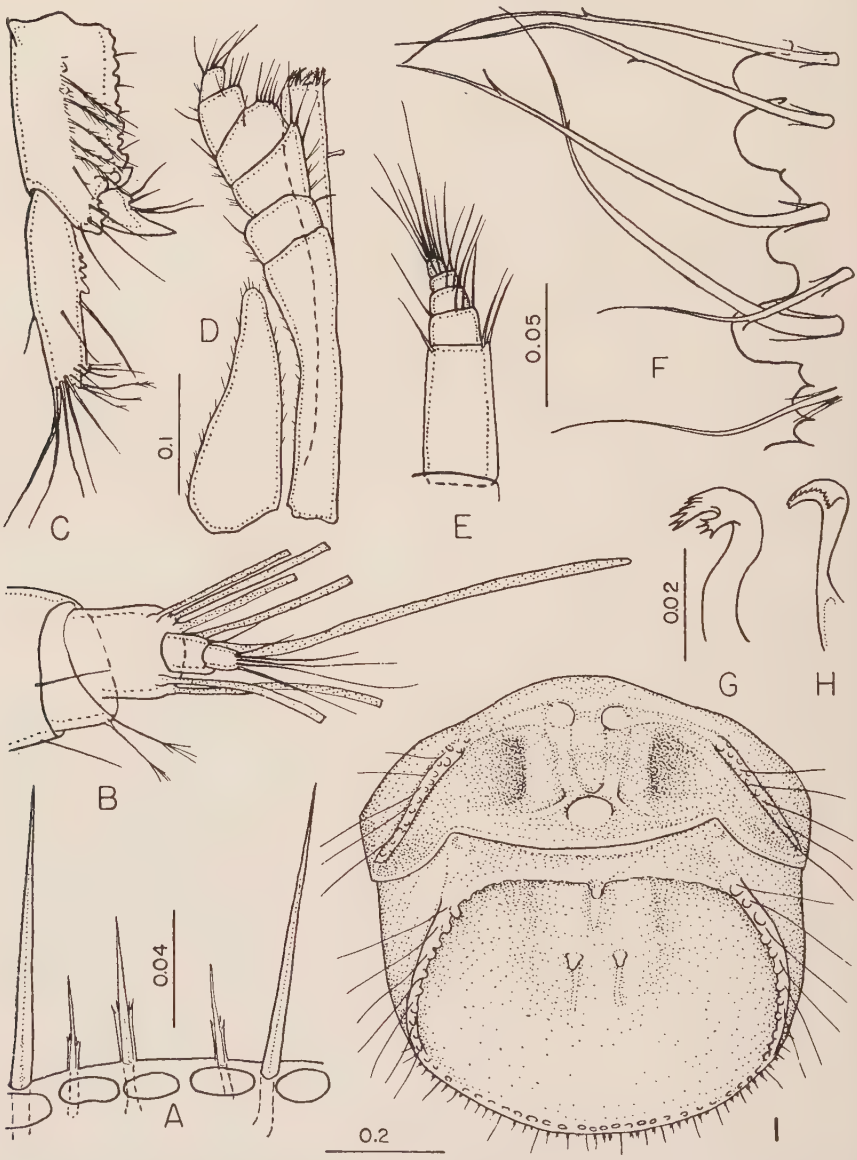

FIGURE 16. *Limnoria (L.) tripunctata* Menzies (from Menzies, 1951), paratype male. A, posterior edge of pleotelson. B, distal articles of first antenna. C, uropod. D, maxilliped. E, flagellum of second antenna. F, lateral crest of pleotelson. G-H, lacinioid seta of right mandible. I, pleotelson. Figures with similar magnification, A; B, E, F; C, D; G, H; I. (after Menzies, 1951)

collected from the Indian Ocean, is known in the Americas only from Miami, Florida.

5. *Limnoria (Limnoria) tripunctata* Menzies

Figure 16

Synonymy:

Limnoria tripunctata Menzies, 1951a, pp. 86-88, pl. 36.

Limnoria lignorum (Rathke). Allen and Carter, 1924, pp. 181-196. Anonymous, 1918, p. 58.—Coker, 1923, pp. 95-100.—Kofoid and Miller, 1927, pp. 308, 331 (in part).—Mohr and LeVeque, 1948, p. 26 (Newport reference).—Richardson, 1899, pp. 821-822 (H. Hemphill's specimens), 1900, p. 222 (South Carolina reference); 1905, pp. 268-279 (San Diego, California and Florida reference in part).—Shackell, 1923, pp. 221-230, figs. 1-4.—Shoemaker, 1949, pp. 1-13 (probable).

Limnoria terebrans, Leach, Gould, 1841, p. 338, (Massachusetts reference).

Diagnosis. Flagellum of second antenna with five articles. Epipod of maxilliped triangulate, two and one-half times as long as wide, just reaching the articulation of the palp with endopod. Mandibular palp with three articles. Dorsal surface of fifth somite of pleon medially with two anteriorly located elevated nodes and a single posteriorly elevated area; central part depressed. Pleotelson medially with one anteriorly located tubercle followed by a pair of tubercles, each of which is followed by a longitudinal carina. Dorsal surface of posterior margin of telson tuberculate, spike-like bristles lacking. Lateral crests conspicuously tuberculate. Lacinioid seta of right mandible abruptly curved distally bearing two prominent flattened, apically spinulate projections.

Type locality. San Diego County, Mission Bay, California. Collected by Mr. and Mrs. R. J. Menzies, December 23, 1948. Types are located in the United States National Museum, British Museum (Natural History) and the Rijksmuseum van Natuurlijke Historie, Leiden.

Measurements. Holotype male length 2.0 mm, width of telson (= pleotelson) at widest point 0.6 mm. Allotype length 2-4 mm, width of pleotelson 0.6 mm (Menzies, 1951, p. 86).

Remarks. In the original description the nodes and elevations on the fifth somite of the pleon were reversed from their actual location. This feature is evident from the figure (Menzies, op. cit., pl. 30, fig. i). It is correctly described in the above diagnosis.

This species has been collected frequently from the creosoted part of treated piling and has been often associated with cases of premature failure of creosoted piling in the United States (Menzies, 1951c, pp. M5-M6). This relationship might be due to the development of creosote tolerant strains of this species, to its being more tolerant originally,

or perhaps more simply, to a more rapid leaching of the creosote in the warm water where this species is found.

Material examined. Including the type series (Menzies, 1951, pp. 86-88), specimens were examined from:

United States

Atlantic Coast.

Rhode Island, April 7, 1948, 2 specimens, W.F.C.L.

Massachusetts, *Boston,* August 9, 1948, 1 specimen, W.F.C.L.

New York, *New York Harbor,* Fisher's Island, October 1, 1948, 7 specimens, W.F.C.L. Sheepshead Bay, August 28, 1950, 50 specimens, H. N. Blume.

North Carolina, *Wilmington, South Port,* and *Kure Beach,* 1948, 1949, 1950, 151 specimens, W.F.C.L.

Bermuda, U. K., May 11, 1948, 15 specimens, W.F.C.L.

Florida, *Mayport, Fort Pierce,* 6 samples, 1949, 1950, 65 specimens, W.F.C.L.; *Miami Beach,* September 1, 1950, 25 specimens, Univ. Miami Marine Laboratory, Leonard Greenfield (with specimens of *L. (L.) pfefferi* and *L. (L.) saseboensis*).

Gulf of Mexico and Caribbean.

Florida, *Key West,* 1948, 1949, 8 specimens, W.F.C.L. *Panama City,* 1949, 1950, 8 specimens, W.F.C.L.

Texas, *Galveston, Corpus Christi,* 1948-1949, 22 specimens, W.F.-C.L. *Port Aransas,* 3 samples, 1948, 1949, more than 100 specimens, J. W. Hedgpeth (in creosoted wood).

Costa Rica. *Limon,* U.S.N.M. Cat. No. 39862, W. C. Mullins, over 100 specimens (identified by Harriet Richardson as *L. lignorum*).

Puerto Rico, *Mona Island,* January 15, 1950, 12 specimens, W.F.-C.L.

Cuba. *Guantanamo Bay,* 1949, U.S. Navy, over 100 specimens from creosoted wood.

Venezuela, *Amuay,* May, 1949, 37 specimens, W.F.C.L.

Pacific Coast.

California, *San Francisco Bay,* San Rafael, McNear's Beach, Sobrento, San Quentin, San Rafael Ferry slip, Belvidere (with *Chelura* and *L. (L.) quadripunctata*), San Mateo, Dumbarton Bridge, both approaches, South Double Basin, Parr-Richmond Pier, Berkeley Yacht Harbor, (with *L. (L.) quadripunctata*), Richmond, San Rafael Ferry Slip, Rodeo (in hole in telegraph pole), April-May 1950, over

100 specimens, R. J. Menzies; Berkeley Yacht Harbor, September 1950, 25 specimens, Dr. J. L. Mohr (with *L. (L.) quadripunctata*). *Port Hueneme,* January 6, 1950, 19 specimens, W.F.C.L. *Los Angeles-Long Beach Harbors,* 1949-1950, several hundred specimens from 14 different localities, Southern California Marine Borer Council. *Newport Bay,* upper part and at Highway 101, 1947, 50 specimens, Dr. J. L. Mohr, and February 14, 1950, 200 specimens. *Catalina Island,* July 15, 1950, 100 specimens, Allan Hancock Foundation (in creosoted timber). *La Jolla,* August 16, 1949, 25 specimens, R. J. Menzies (with *L. (L.) quadripunctata*).

Mexico. Pacific coast; *Ensenada,* September 7, 1949, 35 specimens, Allan Hancock Foundation. *San Quintin Bay,* April 7, 1950, 28 specimens, R. J. Menzies.

Gulf of California, *Santa Rosalia, La Paz harbor, San Marcos Island,* January 1-2, 1954, several hundred specimens, Drs. Gifford C. Ewing and R. J. Menzies.

Mexican mainland; *Mazatlan,* January 2, 1954, about 50 specimens, Drs. Gifford C. Ewing and R. J. Menzies.

Geographical Distribution. On the Atlantic coast from 44°N (Rhode Island, U.S.A.) to 12°N (Amuay, Venezuela) including the Gulf of Mexico; on the Pacific Coast from about 37°N (San Francisco area) to 23°N (Mazatlan, Mexico). The species appears to inhabit water ranging in mean temperature between 15°C and 30°C. It can be considered the most widely distributed species in Northern and Central America.

Limnoria (Limnoria) platycauda, new species

Figure 17

Diagnosis. Flagellum of second antenna with four articles. Epipod of maxilliped reaching nearly to the articulation between the first and second articles of palp; epipod semi-spatulate, narrowest at distal end, about three times as long as wide. Mandibular palp with three articles. Fifth somite of pleon dorsally with a median longitudinal ridge. Pleotelson dorsally lacking ridges or rugosities; posterior margin tuberculate, with few setae and no spike-like bristles. Lateral crests with conspicuous tubercles. Lacinioid seta of right mandible elongated, abruptly bent at distal end which bears a cup-shaped serrated apex.

Type locality. Mouth of Curacao Harbor, Dutch West Indies, J. W. Gonggrip, 1923. Specimens in greenheart timber, collector's note "planks 5 x 25 cm wholly severed at water line." Holotype, allotype, and 97 paratypes returned to the United States National Museum, Cat. No. 59975.

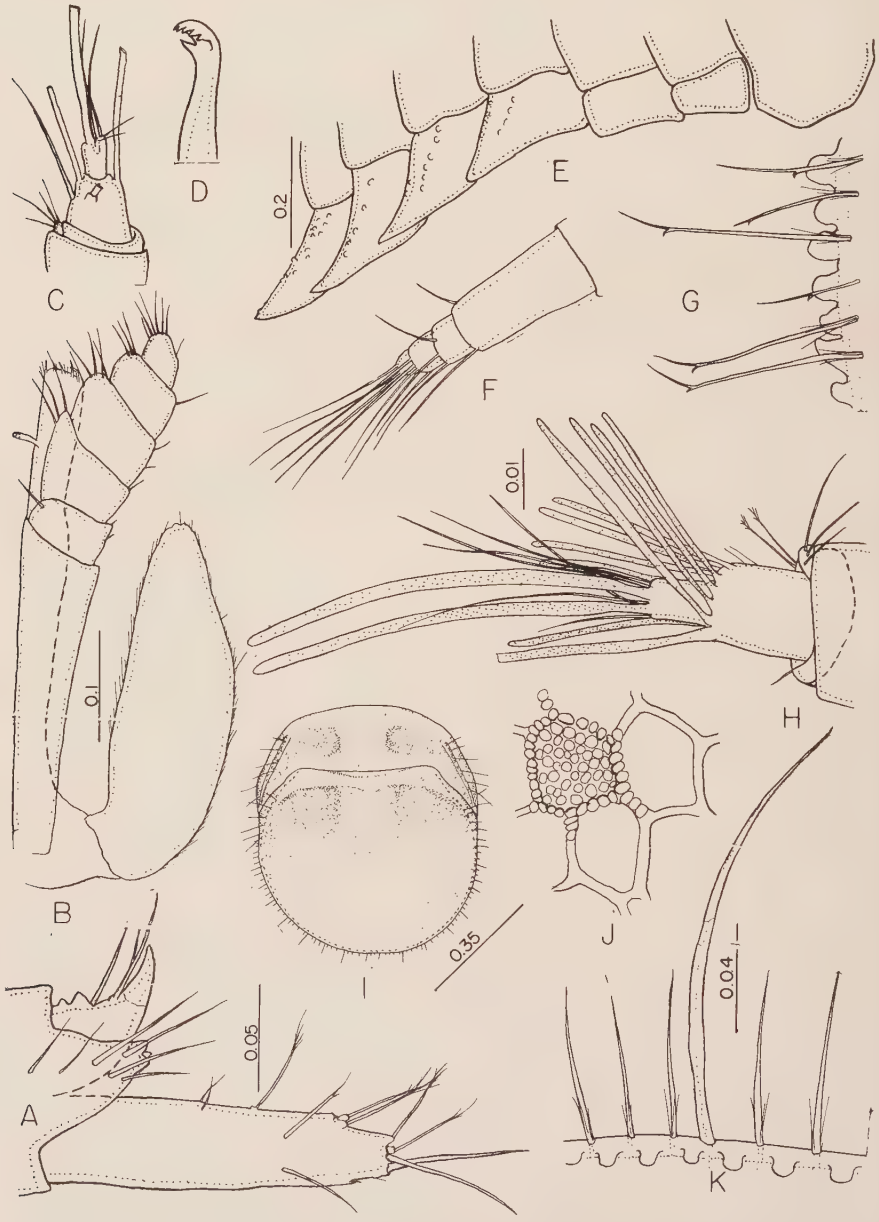

FIGURE 17. *Limnoria (L.) platycauda,* new species, paratype. A, uropod. B, maxilliped. C, distal articles of first antenna. D, lacinioid seta of right mandible, magnification not known. E, lateral margin of peraeon. F, flagellum of second antenna. G, lateral crest of pleotelson. H, distal articles of first antenna. I, pleotelson. J, dorsal surface of pleotelson. K, posterior margin of pleotelson. Figures with similar magnification, A, C, F, G; B; E; H; I; J, K.

Measurements. Holotype male length, 2.0 mm; pleotelsonic width 0.55 mm. Allotype length, 2.0 mm; pleotelsonic width 0.5 mm. Large paratype length, 2.5 mm; pleotelsonic width 0.7 mm.

Remarks. The dorsal surface of pleotelson has few setae or bristles, and thus the underlying structure of the integument is revealed. This consists of small hexagonal areas filled with minute globular bodies which appear more heavily calcified than the rest of the exo-skeleton. In this regard the species resembles *L. (L.) simulata* to a considerable degree. The species differs from all others noticeably in its lack of ridges, rugosities, or tuberculations on the dorsal surface of its pleotelson.

Material examined. In addition to the types, four specimens were examined from Mona Light, Puerto Rico, November 19, 1948, W.F.-C.L.

Geographical distribution. Caribbean, Puerto Rico to Curacao, Dutch West Indies.

Limnoria (Limnoria) saseboensis, new species
Figure 18

Diagnosis. Flagellum of second antenna with five articles. Epipod of maxilliped short, not reaching the articulation of palp with endopod by a distance about equal to 1/3 of its length; epipod strap-like, apically pointed being two and one-half times as long as wide, basal portion widest. Mandibular palp with three articles. Dorsal surface of fifth somite of pleon medially with a pair of subparallel longitudinal carinae which approach one another posteriorly. Pleotelson with two parallel carinae in dorsal surface; carinae tuberculate anteriorly and less so posteriorly; posterior edge tuberculate, margin with spike-like bristles; lateral crests tuberculate. Lacinioid seta of right mandible with two medially curved teeth at apex.

Type locality. The holotype and 11 paratypes were collected at Sasebo, Japan, August 22, 1949, W.F.C.L. With them were specimens of *L. (L.) tripunctata.* These have been sent to the United States National Museum.

Measurements. Holotype male, length 3.5 mm, width of pleotelson 0.95 mm.

Remarks. In having a pentarticulate second antennal flagellum and a tuberculate pleotelsonic margin this species resembles *L. (L.) tripunctata.* It differs markedly from the latter in having an unusually short maxillipedal endopod and parallel carinae on the dorsal surface of fifth somite of the pleon and pleotelson.

Material examined. In addition to the types, six specimens collected

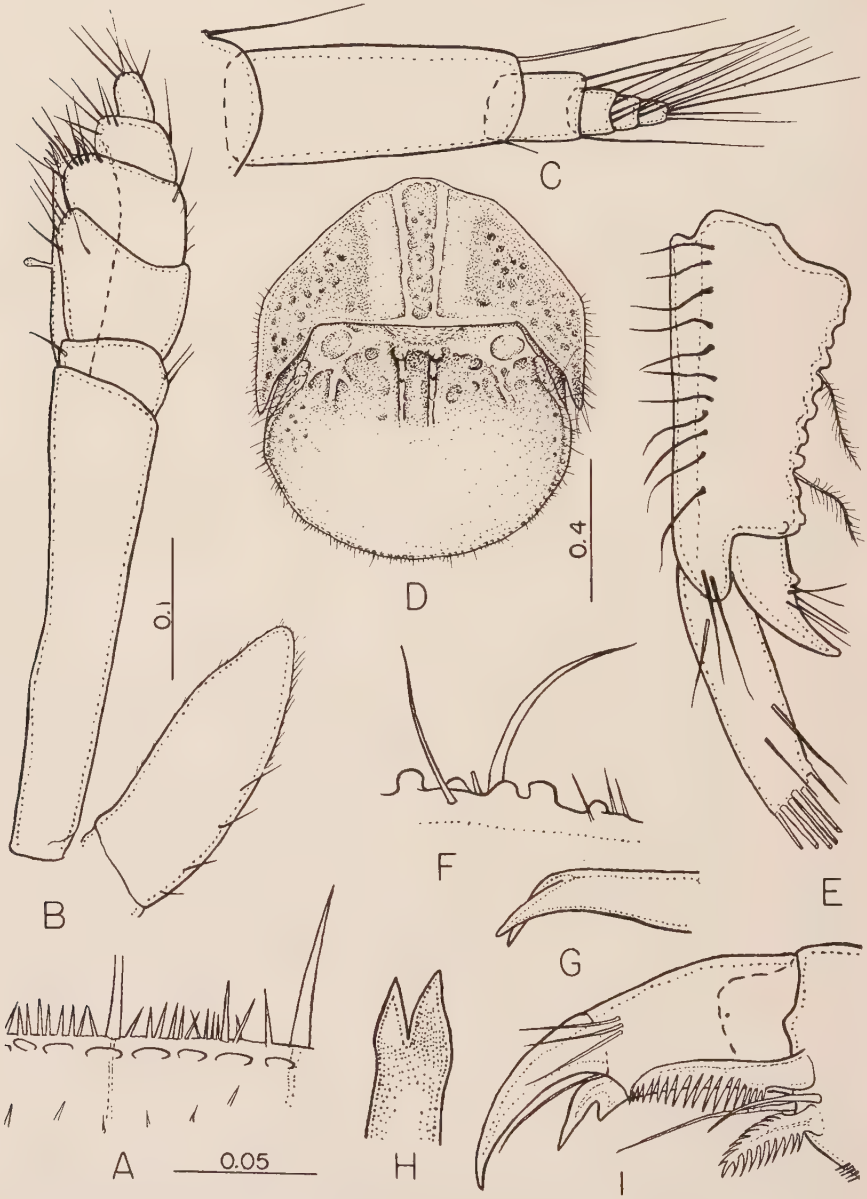

FIGURE 18. *Limnoria (L.) saseboensis,* new species, paratype. A, posterior margin of pleotelson. B, maxilliped. C, flagellum of second antenna. D, pleotelson. E, uropod. F, lateral crest of pleotelson. G, lacinioid seta of right mandible, lateral view. H, lacinioid seta of right mandible, medial view. I, distal articles of first peraeopod. Figures with similar magnification, A, F, I; B, C, E; D-, H, G (magnification not known).

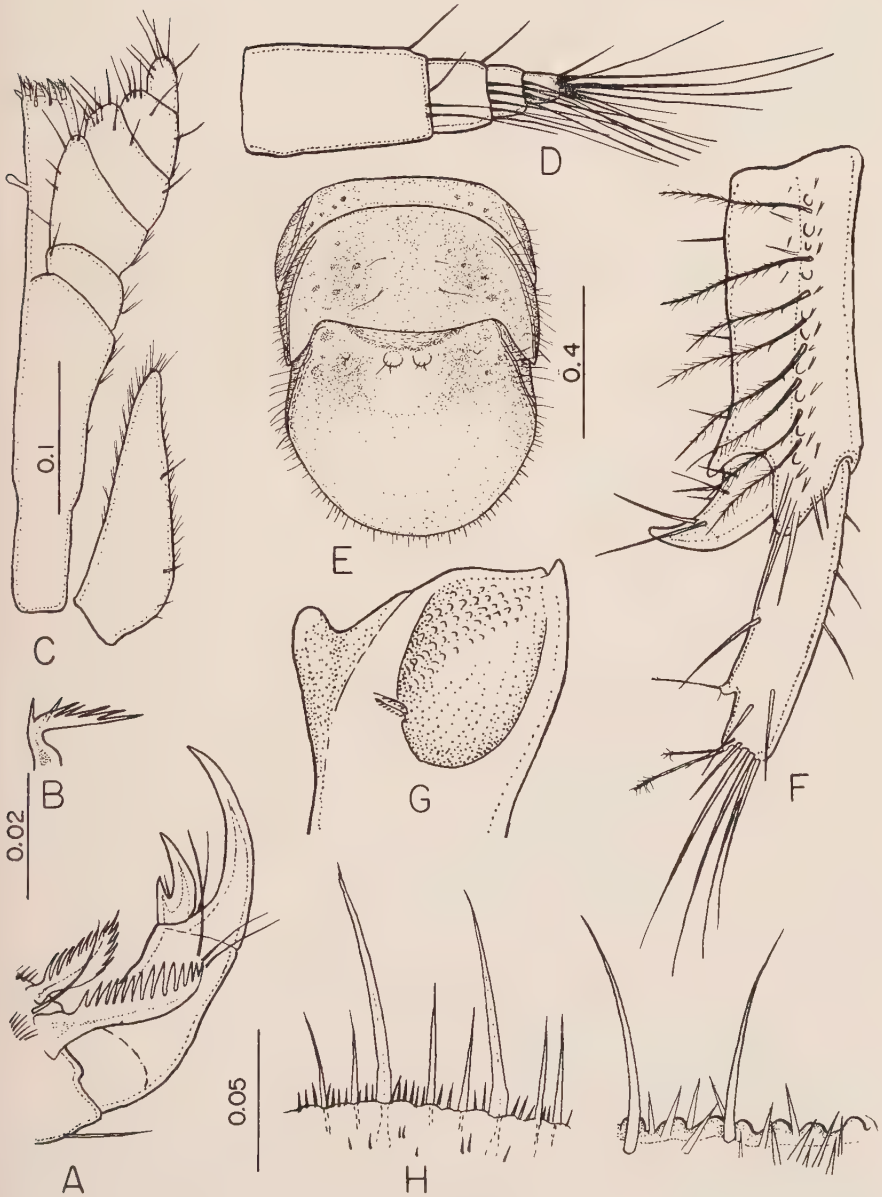

FIGURE 19. *Limnoria (L.) simulata*, new species, male paratype. A, distal articles of first peraeopod. B, lacinioid seta of right mandible. C, maxilliped. D, flagellum of second antenna. E, pleotelson. F, uropod. G, inner surface of left mandible, palp not shown. H, posterior margin of pleotelson. I, lateral crest of pleotelson. Figures with similar magnification, A, D, G, H, I; B; C-, E.

from the county causeway, Miami Beach, Florida, by Mr. Leonard Greenfield, September 1, 1950.

Geographical distribution. Known only from Miami, Florida, and Sasebo, Japan.

Limnoria (Limnoria) simulata, new species
Figure 19

Diagnosis. Flagellum of second antenna with four articles. Epipod of maxilliped triangulate, elongated, reaching to the articulation of first article of the palp with endopod; epipod three times as long as wide. Mandibular palp with three articles. Dorsal surface of fifth somite of pleon with a medial longitudinal sulcus. Dorsal surface of pleotelson with a pair of conspicuous tubercles on either side of the mid-line at anterior end lateral to each of which is a small tubercle; posterior margin irregular, lacking tubercles; lateral crests tuberculate. Lacinioid seta of right mandible provided with elongated spinules.

Type locality. Holotype male from Virgin Islands, West Indies, September 24, 1913 and one paratype male February 16, 1914. These have been returned to Dr. Torben Wolff, Universitetets Zoologiske Museum, Kopenhagen, Denmark.

Measurements. Holotype male length, 3.0 mm, width of pleotelson 0.55 mm.

Remarks. Although there were no data on the label indicating the habitat of this species, the mandibular structure would suggest that it is a wood-borer.

In over-all structure this species resembles *L. (L.) platycauda,* also a Caribbean species. It differs markedly from the latter in lacking a mid-longitudinal ridge on the dorsal surface of the fifth somite of the pleon and in having tubercles on the dorsal surface of the pleotelson which *L. (L.) platycauda* lacks.

Geographical distribution. The species is known only from the Virgin Islands.

Subgenus *Phycolimnoria,* new subgenus

Diagnosis. Members of the genus *Limnoria* (sensu lato) which lack a "rasp" and "file" arrangement of scales and ridges on the incisive process of the mandibles. All known species bore into sea weeds.

Type species. *Limnoria (Phycolimnoria) algarum* n. sp.

This subgenus includes the algal boring parasites, whose characteristic burrows were described on p. 109. Here only one species is treated, e.g. *L. (P.) algarum.* The other known species are *L. (P.) segnis* (Chilton, 1883, pp. 76-77) from Lyttelton Harbor, New Zealand which has a biarticulate mandibular palp and *L. (P.) antarctica* (Pfeffer, 1887, pp. 96-102) from the South Georgia Islands

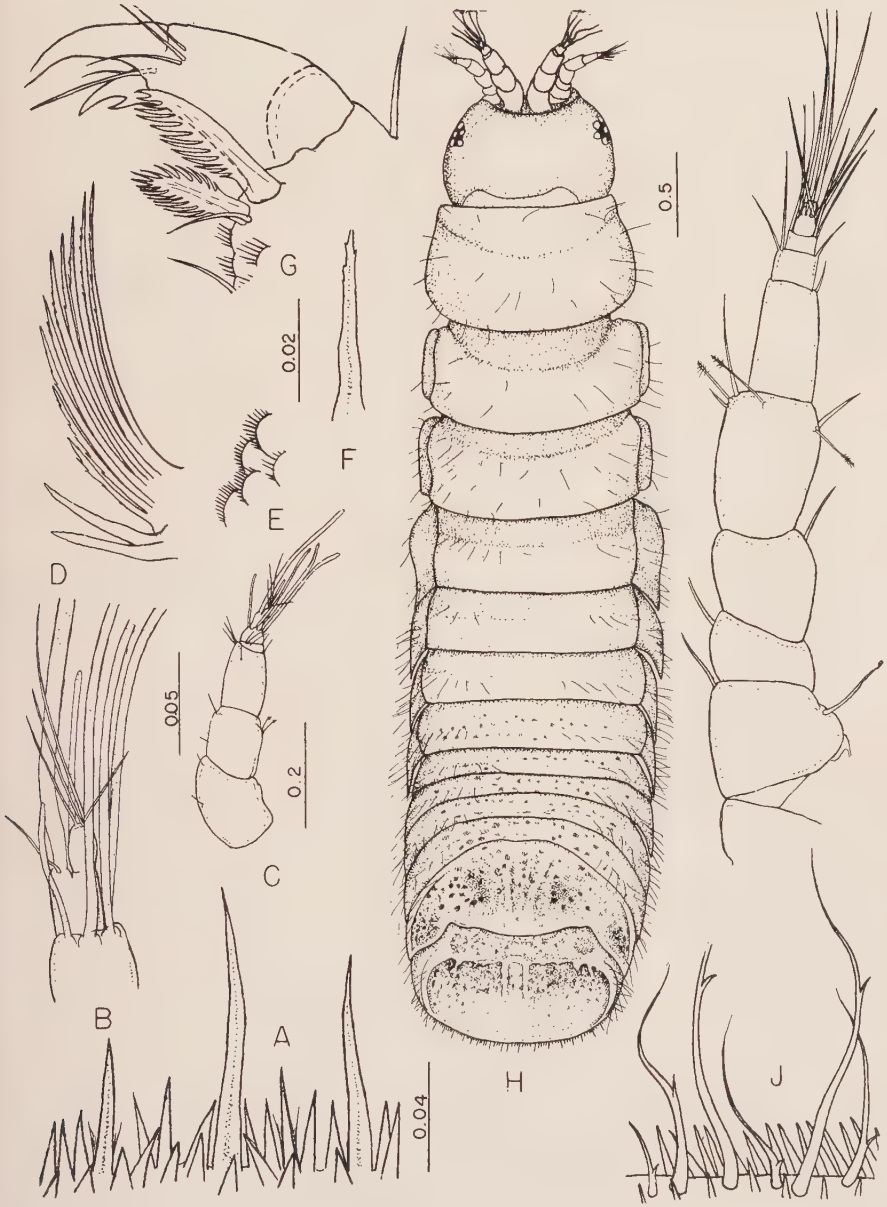

FIGURE 20. *Limnoria (P.) algarum*, new species, paratype. A, posterior margin of pleotelson. B, distal articles of first antenna. C, first antenna. D, setal row. E, scales of first antenna. F, lacinioid seta of setal row of right mandible. G, distal article of first peraeopod. H, *in toto*, dorsal view. I, second antenna. J, lateral crest of pleotelson. Figures with similar magnification, A; B, E, G, J; C; D, F; H; I.

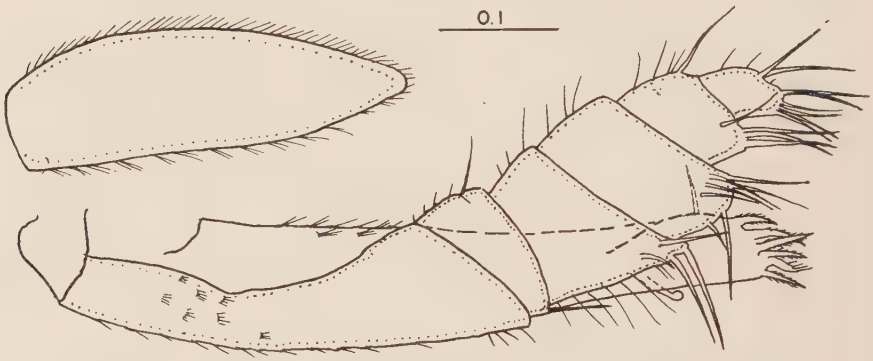

FIGURE 21. *Limnoria (P.) algarum,* new species, paratype, maxilliped.

in the Antarctic which like *L. (P.) algarum,* has a triarticulate mandibular palp. The two latter species may be distinguished from one another by the fact that the flagellum of the second antenna has four articles in *L. (P.) antarctica* and five in *L. (P.) algarum.*

The species thus far have been taken from nine genera of kelps (Laminariales), *Egregia, Macrocystis, Neriocystis, Laminaria, Sargassum, Lessonia, Lessoniopsis, Postelsia,* and *Eisenia.*

Limnoria (Phycolimnoria) algarum, new species
Figures 20-21

Diagnosis. Flagellum of second antenna with five articles. Epipod of maxilliped reaching the articulation of first article of palp with endopod; epipod strap-like, being three and one-half times as long as wide. Mandibular palp with three articles. Dorsal surface of fifth somite of pleon medially with a V-shaped carina. Dorsal surface of pleotelson medially with two weak parallel carinae. Pleon and pleotelson foveolate, posterior border fringed with many spike-like bristles and long setae; lateral crests and posterior margin lack tubercles. Lacinioid seta of right mandible simple, pointed, distally spinulate and not vastly different from other setae of the setal row.

Type locality. Dillon Beach, Marin County, California, April 25, 1949, 15 specimens from holdfasts of *Macrocystis* and *Egregia,* R. J. Menzies.

Measurements. Holotype male, length 3.00 mm, width of pleotelson 0.9 mm. Allotype (ovigerous), length 5.5 mm, width of pleotelson 1.0 mm.

Remarks. Besides differing from the two other known species in the number of articles comprising the flagellum of the second antenna and mandibular palp the ornamentation of the fifth somite of the pleon and pleotelson is further unique.

Material examined. Exclusive of the types, specimens were examined from the following localities all along the Pacific coast of North America.

Oregon. *Squaw Island,* Cape Arago, August 25-26, 1950, 55 specimens. Dr. J. L. Mohr; Gregory Point, August 27, 1950, 42 specimens, Dr. J. L. Mohr.

California. *Marin County,* Tomales Point and Duxbury Reef, July. August 1948, 15 specimens, Miss M. Barr. *Morro Bay,* San Luis Obispo Co., February 1-2, 1950, 13 specimens, R. J. Menzies and Dr. J. L. Mohr. *Point Fermin,* Los Angeles Co., February 14, 1949, 18 specimens, Dr. J. L. Mohr. *La Jolla,* San Diego Co., July 1953, about 50 specimens, R. J. Menzies.

Geographical Distribution. Oregon to Southern California, in holdfast of the algae *Egregia, Eisenia, Laminaria, Macrocystis,* and *Postelsia.*

Genus *Paralimnoria,* new genus

Diagnosis. Flagellum of first antenna with five articles. Flagellum of second antenna with five or six articles. Mandibular incisive processes with a "rasp" and "file" wood-boring apparatus. Lacinioid seta of right mandible tubular, with an apical circle of spines. Exopod and endopod of uropods subequal in length (exopod slightly shorter than endopod), each provided with a pointed spine-like (claw) apex, lateral margins of uropods with peculiar setae (Fig. 7) which do not occur in the genus *Limnoria* (sensu lato). Fifth pair of pleopods with marginal setae.

Type species. *Limnoria andrewsi* Calman, 1910, pp. 184-186, pl. V.

Distribution. In the Americas the genus appears to be restricted to Caribbean waters. The type species was described originally from the Indian Ocean.

Remarks. Only the type species is known to belong to this genus. This, however, presents some marked variations and may be divided into three *formae.* This term is used here to indicate a usually distinctive variation within one species or subspecies the cause of which is not known and which shows no evident correlation with ecologic, genetic, or geographic information.

When describing *L. andrewsi,* Calman (op. cit.) noted that the fifth pair of pleopods had marginal setae. He, therefore, modified Hansen's (1905, p. 98) diagnosis of the subfamily Limnoriinae (here considered a family). Calman did not observe the claw-like ends of each uropodal branch which are important characteristics separating the genus from *Limnoria* (sensu lato).

The conspicuous scale attached to the first antenna of *Paralimnoria* is also characteristic of the genus *Limnoria* and as Calman remarks

of the genus *Bathynomus* (suborder Flabellifera) and cryptoniscian larvae (suborder Bopyroidea). It has since been found on *Mesantheura* (suborder Anthuridea, Miller and Menzies, 1952, p. 8) and the young of *Cirolana* (unpub. data) and it is possibly characteristic of isopods in general.

Paralimnoria andrewsi (Calman)
Figures 22-24

Synonymy:

Limnoria andrewsi Calman, 1910, pp. 184-186, pl. V, figs. 7-14. —Atwood and Johnson, 1924, pp. 24-25, pl. 1, figs. 3-5. Chilton, 1914a, pp. 382-387.—Holthuis, 1949, p. 170.—Kofoid and Miller, 1927, pp. 309, 331.—Miller, 1924, pp. 159-164.

Diagnosis. Flagellum of second antenna with five-six articles. Epipod of maxilliped slightly exceeding the articulation of first article of palp with endopod; epipod apically pointed, about two and two-thirds as long as wide. Mandibular palp with three articles. Ornamentation of dorsal surface of fifth somite of pleon and pleotelson variable. Lacinioid seta of right mandible tubular, bent near apex which is serrated around margins and has a central tooth.

Type locality. Christmas Island, Indian Ocean, 1908, collected by Dr. C. W. Andrews. Found in piles of pier at Flying Fish cove with the amphipod *Chelura insulae* Calman (Calman, 1910). Types located in the British Museum (of Natural History).

Formae

Three formae are recognizable, *Forma typica* (Calman's types), *Forma A* and *Forma B*. As a rule one sample contained specimens of only one forma; however, in some cases (not reported here) two formae occurred together. In some samples the characteristics of the formae seemed so mixed that a precise assignment was not possible.

Forma *typica*
Figures 22-24

Diagnosis. Fifth somite of pleon lacking central depressed triangulate area. Pleotelson dorsally with a pair of elevated tubercles near center, each followed posteriorly by a short, obscure carina. Lateral crest of pleotelson tuberculate, posterior margin sparsely tuberculate in most instances.

Specimens examined. Two female cotypes described by Calman (1910).

Forma *A*
Figure 24 A

Diagnosis. Fifth somite of pleon with a central depressed triangulate area. Pleotelson dorsally with a pair of elevated tubercles each followed posteriorly by a long carina which extends almost to the distal margin of pleotelson. Lateral

crests and posterior margin of telson markedly tuberculate.

Specimens examined. Curacao, Dutch West Indies, 1923, 11 specimens, J. W. Gonggryp in greenheart timber with L. *(L.) platycauda* (p. 35), U.S.N.M. Cat. No. 59975.

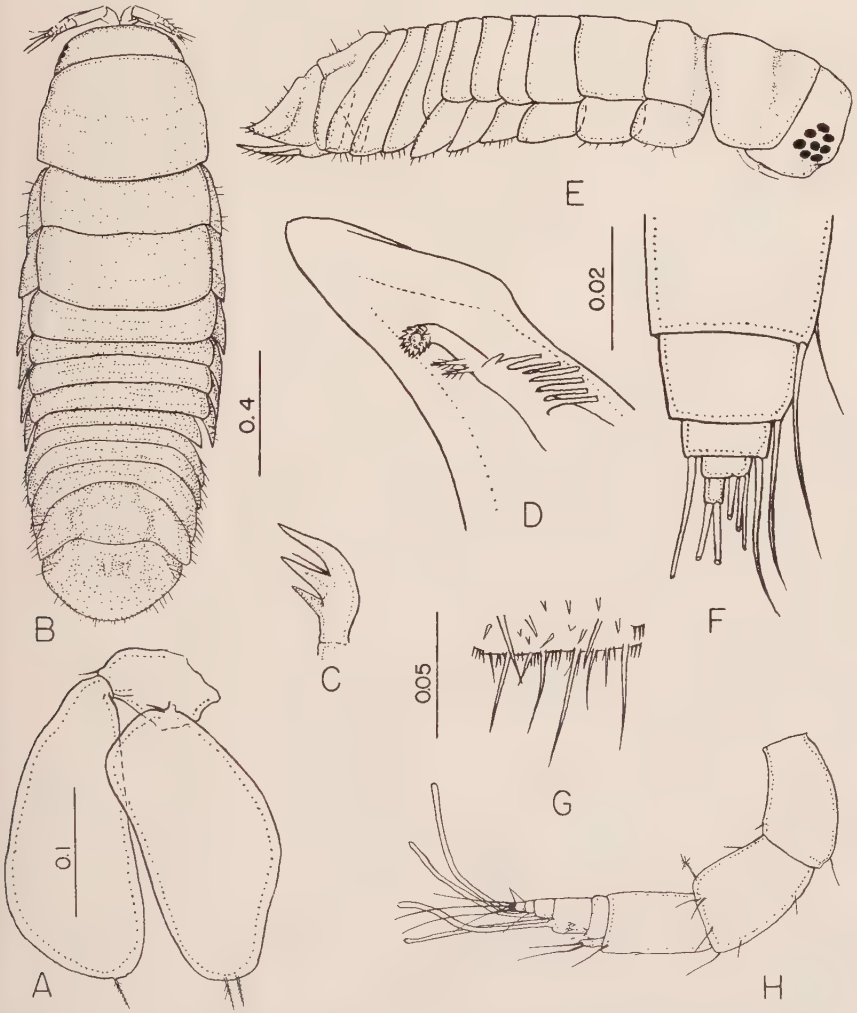

FIGURE 22. *Paralimnoria andrewsi* (Calman). A, fifth pleopod. B, *in toto,* dorsal view. C, accessory claw of first peraeopod. D, inner surface, right mandible. E, *in toto,* lateral view. F, apical articles of second antenna. G, apex of pleotelson. H, first antenna. Figures with similar magnification, A; B, E; C, D, F; G, H.

FIGURE 23. *Paralimnoria andrewsi* (Calman). A, maxilliped. B, right mandible. C, eye, lateral view. D, distal articles of first peraeopod. E, uropod. Figures with similar magnification, A, B, C, E; D.

Forma *B*

Diagnosis. Fifth somite of pleon with a central depressed area. Pleotelson as described for forma *typica*.

Specimens examined. Key West, Florida, April 4, 1949, 5 specimens, W.F.C.L.

Remarks. Calman (1910, fig. 7) did not indicate the evident coxal plates of this species and incorrectly figured the flagellum of the antennae. Beyond these corrections and those previously cited (p. 42) Calman's description is very accurate.

Distribution. In addition to the Caribbean localities mentioned, the species has been recorded from Samoa and the Hawaiian Islands (Miller, 1924) and Misaki and Tanabe Bay, Japan (Shiino, 1950).

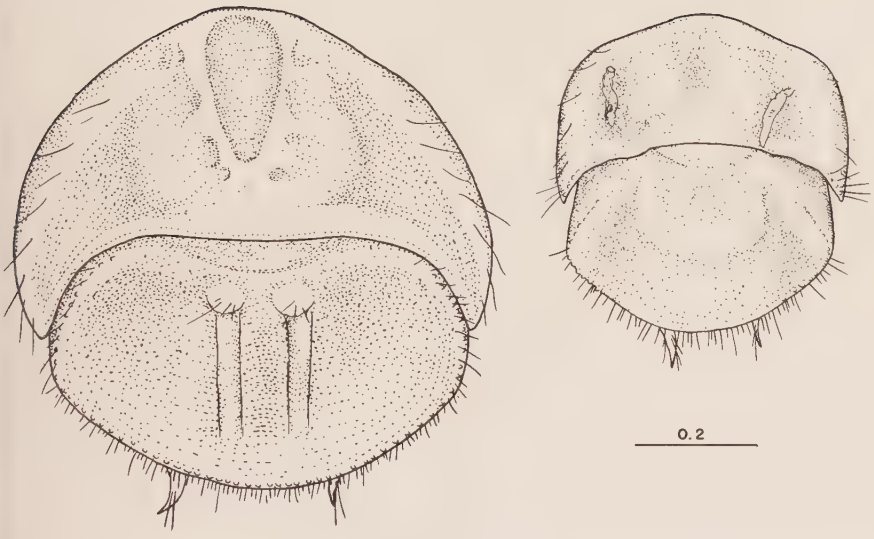

FIGURE 24. *Paralimnoria andrewsi* (Calman). A, pleotelson, forma B. B, pleotelson, forma typica; note protozoans on fifth somite of pleon. Magnification, both to same scale.

It accordingly appears to be a widely distributed (cosmopolite) tropical species.

DISTRIBUTION

The geographic distribution of individual species has already been given in detail as part of each description. Here distribution is treated in more general terms with emphasis on similarities and differences between species and with particular attention to the factors which appear to limit their distribution.

General

The collections of gribbles seem reasonably complete on the Pacific coast from Alaska to Mazatlan, Mexico and on the Atlantic coast from Maine to Miami, Florida. Outside of these areas the collections are spotty and the conclusions that may be drawn become more tentative (Figure 25).

The genus *Paralimnoria,* as far as North America is concerned, appears restricted to the Caribbean region, but might be expected to occur along the west coast of Central America in view of its wide distribution elsewhere.* The species *Limnoria (L.) platycauda, L. (L.)*

*unpublished data.

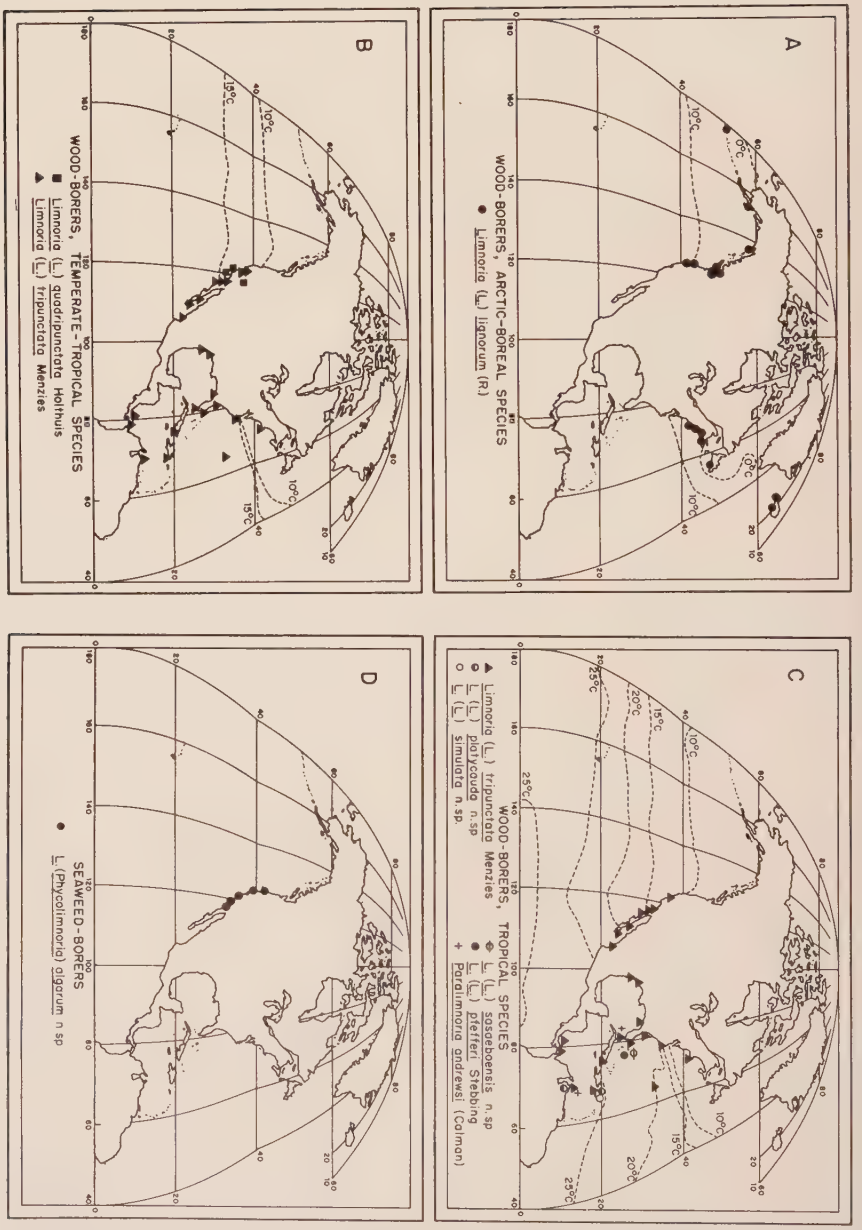

FIGURE 25. The distribution of the Limnoriidae in Northern and Central America. A, wood-borers, arctic-boreal. B, wood-borers, temperate-tropical species. C, wood-borers, tropical species. D, seaweed borers.

saseboensis, L. (L.) pfefferi, and *L. (L.) simulata* which also are known from other tropical regions, have a similar distribution. The apparent restriction of the species *L. (Phycolimnoria) algarum* to the Pacific Coast of North America may well be due only to a lack of any search for it on the Atlantic Coast. The genus at least may be suspected to occur wherever Laminariales grow. The following summarizes the general distribution of the American species.

Pacific Coast: four species.

1. *Limnoria (Limnoria) lignorum*
2. *Limnoria (Limnoria) quadripunctata*
3. *Limnoria (Limnoria) tripunctata*
4. *Limnoria (Phycolimnoria) algarum*

Atlantic Coast: four species (excluding Caribbean and Gulf of Mexico)

1. *Limnoria (L.) lignorum*
2. *Limnoria (L.) tripunctata*
3. *Limnoria (L.) pfefferi*
4. *Limnoria (L.) sasaeboenses*

Caribbean and Gulf of Mexico: four species

1. *Limnoria (L.) tripunctata*
2. *Limnoria (L.) platycauda*
3. *Limnoria (L.) simulata*
4. *Paralimnoria andrewsi*

Species common to both coasts: two species

1. *Limnoria (L.) lignorum,* a boreal circumpolar species
2. *Limnoria (L.) tripunctata,* a temperate-tropical cosmopolite

Factors Associated with the Distribution of Limnoria.

The environmental factors which are suspected or known to influence the distribution of *Limnoria* are food, depth with associated phenomena, dissolved oxygen, salinity, and temperature.

1. *Food.* The food supply of *Limnoria* is restricted either to seaweeds (subgenus *Phycolimnoria*) or wood (subgenus *Limnoria* and genus *Paralimnoria*). In the laboratory specimens of both subgenera have been kept for over a month on a diet of particulate cellulose in solid agar with no apparent adverse effects, indicating that their dietary requirements might be similar. In nature, however, the subgenus *Limnoria* has not been found in algae nor has *Phycolimnoria* been taken from wood. Members of both subgenera have been found to survive for as long as thirty days in the absence of food.

This ability to withstand starvation no doubt increases the opportunity for the animals to find food in nature. Limnorias have not been found where there was no available food, but on the other hand, areas with ample supplies of wood or kelp were found and although other environmental factors appeared to be ideal for their existence, no *Limnoria* were discovered. For example, drift wood and wooden floats examined along the entire peninsular side of the Gulf of California from Los Angeles Bay to Santa Rosalia Bay were found to be free from *Limnoria* but showed evidence of extensive teredine attack.

2. *Depth.* The extremely limited data available on the vertical distribution of *Limnoria* are such that little can be said about the influence of depth on their distribution. Wood is scarce at great depths and it seems remarkable that the animals are found at all in deep water. The collections on which this report is based were all taken from shallow water, e.g. surface to about 60 feet at a maximum. The species *Limnoria (L.) japonica* Richardson (1909) was reported from a depth of 163 fathoms off Suduz Misaki Light, Japan. Barnard (1936) reports *L. (L.) segnis* Barnard from 185-250 fathoms off the Andaman Islands in the Indian Ocean. Neither of these species has been collected from shallow water. Andrews (1875) recorded an attack by *Limnoria* on the guttapercha covering of a telegraph cable between Holyhead and Ireland. Chilton (1916) gave a similar report of cable damage by *Limnoria* from a depth of 60 fathoms off Sinclair Head in Cook Straight, New Zealand, and Calman (1936) records it from a submarine cable at a depth of 290 fathoms in the Mediterranean. Both Chilton and Calman identified the species with *L. (L.) lignorum* (Rathke) but these determinations are questionable in view of the multitude of species now believed to exist which were not known to those investigators.

3. *Dissolved oxygen.* The dissolved oxygen content of near-shore sea water, except in polluted areas, is rather high. It varies between 4 and 8 parts per million (ppm) in harbors in Southern California and is presumably higher in more northern localities. In Los Angeles-Long Beach Harbor *Limnoria* has been found in sea water whose dissolved oxygen ranged seasonally between 0.0 to 4.0 (mean 1.6) ppm. It was not found at a station where the oxygen concentration ranged seasonally between 0.0-1.4 (mean 0.12) ppm.[1] This suggests

[1]Data supplied through the courtesy of the Southern California Marine Borer Council, Box 786, Wilmington, California.

that an average dissolved oxygen content somewhat below 1.6 ppm might constitute a limiting factor in the survival of *Limnoria*. It was apparent from the data that populations could survive in areas having periodic oxygen depletion.

4. *Salinity*. In nature low salinity appears to be an important factor governing the distribution of *Limnoria*. This is particularly evident near shore in restricted localities where seasonal variations in salinity are common. Laboratory experiments by White (1929) and Henderson (1924, *L. (L.) lignorum*), Coker (1923, *L. (L.) tripunctata*), and Kofoid and Miller (1927, *L. (L.) quadripunctata*) all indicate that the animals cannot survive for more than a day in fresh water. Salinities between 10-18 ‰ had no unfavorable effect for as long as 8-12 days. Long-term experiments were not conducted by those investigators and accordingly the effect of lowered salinity on reproduction or the development of young is not known. The upper salinity limit tolerated by *Limnoria* has not been determined.

Areas having uniformly low salinities (below 10 ‰) and those having wide ranges of salinity (e.g. 0.00 ‰ to 35.00 ‰) might be considered as unfavorable for the development and establishment of *Limnoria*. Field data correlating salinity with the presence or absence of *Limnoria* are not abundant. The agreement with experimental results is far from perfect. As pointed out by Sømme (1940) part of this disagreement is because only surface salinities have been considered; whereas, *Limnoria* may be found at the bottom in water of a higher and more favorable salinity. This is especially well-illustrated in the data given by M'Gonigle (1925) where a surface salinity of 6.98 ‰ contrasted with that of 29.16 ‰ at a depth of only 14 feet at Sheet Harbor, Nova Scotia. The gribble, although scarce, was much more numerous at the bottom than at the surface. Black and Elsey (1948) found *Limnoria* at Shannon Bay, Queen Charlotte Island where the surface salinity was below 8 ‰ for short periods of time during November, January, and March. At Shannon Bay, attack was mild as compared with more saline localities and was markedly greater at the bottom than at the surface.

It is to be noted, however, that almost without exception the attack by *L. (L.) lignorum* was reported by the above investigators to be greatest at the bottom than at surface regardless of the magnitude of the seasonal salinity fluctuations. The wide tidal fluctuations may play an important role in such areas in keeping *Limnoria* attack near the bottom of piling, but there seems little doubt that salinities

as low as 6.0 ‰ would have an adverse effect on *Limnoria* populations.

The gribble, *L. (L.) tripunctata* is not known to occur at the Carquinez Strait, California (vicinity of San Francisco Bay) or farther east in Suisun Bay. At Crockett the surface salinity (Kofoid and Miller, 1927) was below 12 ‰ for five months of the year and below 10 ‰ for four months of the year. Since other factors do not appear to be limiting such low salinity conditions are presumably unfavorable for *Limnoria* at that locality.

Watson *et al.* (1936) did not find *Limnoria* at Kangaroo Point, Port of Brisbane, Australia, where the salinity averaged 16 ‰ but was subject to reductions as low as 2 ‰ for several days during periods of heavy runoff. During dry seasons the salinity rose as high as 28 ‰.

On the other hand *Limnoria* (presumably *L. (L.) lignorum*) is reported by Sømme (1940) to occur on the Danish coast down to Kjels Nor where the yearly average salinity is only 14.3 ‰ with a minimum of 8.6 ‰ for one month and at Neustadt on the German Baltic coast at a salinity of only 9-10 ‰.

Clearly more field data over long periods of time are needed to establish more precisely the natural limits of salinity variations tolerated by *Limnoria*. The animal appears to be moderately euryhaline in its salinity tolerance as compared with other marine organisms.

5. *Temperature*. Variations in temperature appear to have a significant influence on the distribution of *Limnoria*. Temperature above or below an optimal range might adversely effect a species through: killing the adults; not killing the adults but causing a cessation of breeding activity, causing a serious slowing in the rate of egg production, rate of embryonic development, or in impairing the survival rate of gametes, embryos, or larvae, or any combination of these.

Mawatari (1949) found temperatures ranging between 2°C and 6°C to be lethal to adult *Limnoria* (probably *L. (L.) tripunctata*). A cooling of 5°C water to −9°C in the course of 2½ hours was found by Sømme (1940) to result in an 83% kill of *L. (L.) lignorum* in Norway. Temperatures of 2°C-6°C were not found to be lethal to adults of *L. (L.) lignorum*. The important feature here is that each of the two species shows a different limiting temperature for adults. Within the geographic range of *L. (L.) lignorum* temperatures as low as 2°C-6°C are often encountered seasonally. Such is not the case for *L. (L.) tripunctata*.

The breeding of *L. (L.) tripunctata* at Beaufort, North Carolina, is reported by Coker (1923) to cease when temperatures fall below 10°C. Coker also found lower egg numbers during periods of warm water (summer) and cold water (winter) than during periods having intermediate temperatures. Menzies (1954) reports that egg production of *L. (L.) tripunctata* in San Diego Harbor requires about twice as much time at temperatures near 15°C than when temperatures were near 20°C.

Sømme (1940) reports the embryonic development of *L. (L.) lignorum* to be retarded when temperatures fell below 6°C. At 6°C the entire incubation period was estimated to cover about three months rather than the two months needed at higher temperatures. She suggests that at temperatures near zero the brood might survive only in a more or less dormant state.

Both experimental and field data suggest that the reproductive capacities of these species are seriously impaired when the temperature is below a certain limit. For *L. (L.) lignorum* this limit seems near 0°C and for *L. (L.) tripunctata* it appears to be near 6°C. Data on the effect of high temperatures on the activities of the species are scarce. Sømme (op. cit.) reports an average temperature of 24.7°C (over a period of five days) to be unfavorable for the development of embryos of *Limnoria lignorum*.

The distribution of the species sheds some additional light on these problems. The species of *Limnoria* for which abundant collections are available show a northern (cold) and some show additionally a southern (warm) limit to their distribution in the northern hemisphere. Some species appear to have no upper temperature limit as far as temperatures normally encountered in the ocean are concerned. Because species do have geographic limits it is reasonable to suspect, if other ecologic conditions are within tolerable limits, that locations more to the north or south probably have conditions unfavorable for population by that species. Obviously temperature conditions at marginal areas are favorable enough to permit the existence of the species. It seems evident also that temperature conditions within the range of a species are at some points more favorable for its development than at other points (optimal temperature conditions). The precise determination of optimal temperature conditions naturally depends on the results of field studies, laboratory experiments, and detailed natural population analysis correlated with temperature measurements.

In the northern hemisphere four categories of marine animal distribution have been established by students of zoogeography; e.g. arctic, boreal, temperate, and tropical.

Arctic Species

No species of *Limnoria* or *Paralimnoria* is known to have a typical Arctic distribution. The species which has occasionally been found in the Arctic and which occupies the fringe of the Arctic is *Limnoria (L.) lignorum*. From Sømme's data (op. cit.) which suggest that development does not progress at 0°C., it would seem probable that this species is limited by the 0°C isotherm which surrounds the Arctic Ocean. Wood and kelps are largely lacking from the Arctic Ocean and this scarcity of food is perhaps equally as important in keeping *Limnoria* out of the Arctic. Spring and summer melting of ice and the dilution of sea water might also be factors contributing to its absence at least from the surface water. At any rate, low temperature, lack of food, and wide seasonal salinity variations apparently add up to an environment unfavorable for the existence of *Limnoria* in the Arctic.

Boreal Species[2]

Only one species, *Limnoria (L.) lignorum* has a typical boreal distribution (Fig. 25). It is found on the Pacific coast as far north as Sitka, Alaska, and on the Atlantic coast as far north as the western part of Iceland (Stephensen, 1929, p. 16). Presumably at these extreme locations one approaches, seasonally at least, temperature minima tolerable for this species. The seasonal temperature curves for Sitka, Alaska and Eastport, Maine (which is somewhat similar in its temperature to Iceland) are shown in Figure 26. At Sitka the mean seasonal minimum is 4.2°C, the maximum 13.6°C, the mean 8.3°C. At Eastport these values in order are 1.1°C, 11.0°C, and 6.1°C. On the Pacific coast the species extend south as far as Point Arena, California. At Samoa, Humboldt Bay, California it was collected with specimens of *Limnoria (L.) quadripunctata*. Temperature curves are not available for Point Arena, and those for Crescent City, California have accordingly been used. There the minimum temperature is 10.0°C, the maximum 14.0°C, and the

[2]The temperature values given here represent means over a variable number of years depending upon the locality. They are derived from the publications TW-1 and TW-2, U.S. Coast and Geodetic Survey, Washington, D.C., which cover the "Surface water temperatures at Coast and Geodetic tide stations"; 1947 (TW-1, Atlantic and Gulf Coasts) and 1948 (TW-2, Pacific Ocean).

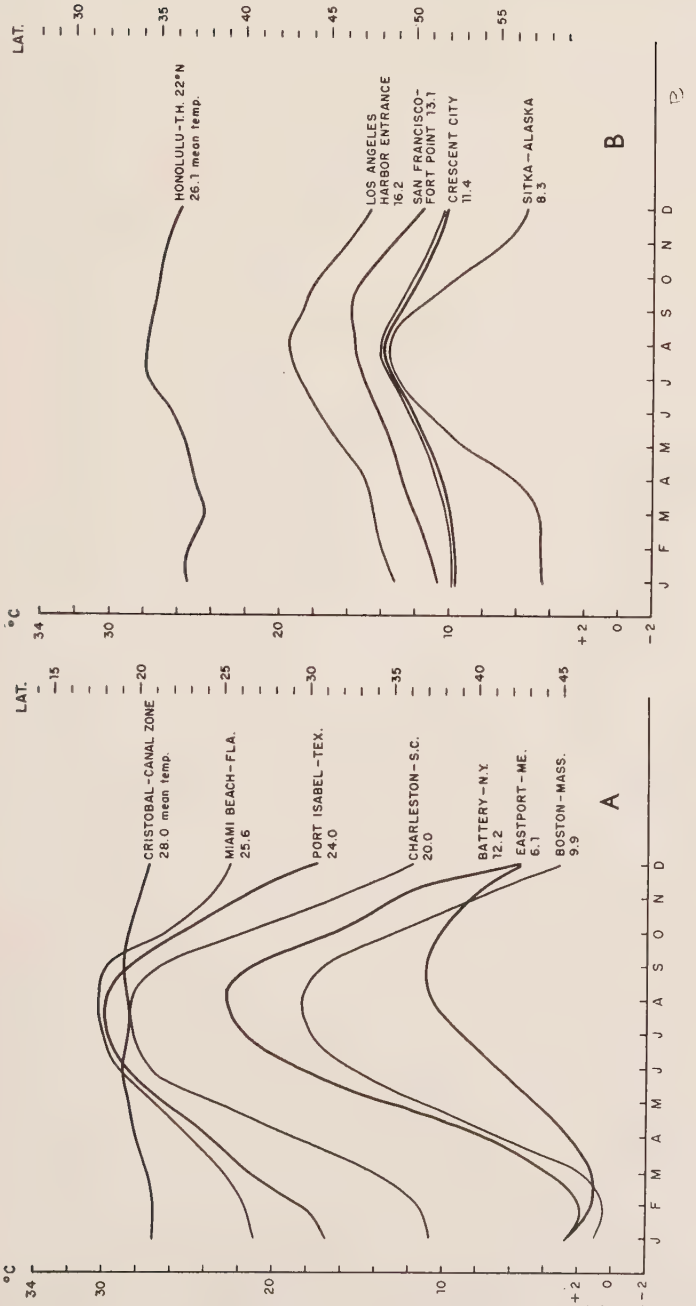

FIGURE 26. The monthly mean temperatures at various localities in America. A, Atlantic Ocean. B, Pacific Ocean.

mean 11.4°C. On the Atlantic coast *L. (L.) lignorum* is known as far south as Boston where the seasonal minimum is 0.4°C, the maximum 18.2°C, and the mean 9.9°C. It is interesting to note that temperatures lethal to adults are not encountered at either place but that low temperatures unfavorable for the development of the young do occur seasonally at all localities. The wide range of temperatures of localities between Boston and Eastport, allowing only a few consecutive months to have optimal temperatures would seem to offer less favorable conditions for *L. (L.) lignorum* than the narrower ranges encountered on the Pacific coast between Point Arena, California and Sitka, Alaska.

Temperate Species

Only one species, *Limnoria (L.) quadripunctata,* shows a temperate distribution. It is found between Humboldt Bay, California and La Jolla, California on the Pacific coast. However, its most southward extent in appreciable numbers is at the outer harbor of Los Angeles-Long Beach Harbors. It is not found on the Atlantic coast and this becomes a matter of considerable interest in view of the high number of collections available from the Atlantic coast. Temperatures from the outer harbor at Los Angeles are taken as representative of those at its southern limits. The minimum, mean and maximum seasonal temperatures at Crescent City are 10.0°C, 11.4°C, and 13.9°C. At Los Angeles harbor comparable values are 13.2°C, 16.2°C, and 19.4°C. If the mean temperatures of 11.4°C and 16.2°C at the extreme localities are assumed to represent limits containing within them an optimal range of temperatures for the development of this species then the absence of it from the Atlantic coast is easily accounted for. On the Atlantic coast from Eastport, Maine to Miami, Florida temperatures within that range are found only two successive months of the year and in total only three months out of the year (Table 2). In contrast within the range inhabited by the species the occurrence of assumed favorable temperatures is much more common; e.g. six months out of the year at Crescent City, seven months out of the year at Los Angeles and eleven months out of the year at San Francisco. At Sitka, Alaska four months of the year have temperatures within that range although the species is not known to occur here. If four successive months of the year having temperatures favorable for the species are insufficient for its establishment then two months of such temperatures, such as occur on the Atlantic coast would hardly seem adequate. Johnson, *et al.* (1947)

indicate that the duration of optimal temperatures appears to be important also in the control of the distribution of the snapping shrimps.

Temperate-Tropical Species

One species, *Limnoria (L.) tripunctata* extends from the temperate to the tropical areas on both coasts. On the Pacific coast its northward limit is San Francisco Bay. Its southward limit has not been defined but it has been collected at Mazatlan, Mexico and does occur in the tropical Pacific at Honolulu, Territory of Hawaii as well as at other islands in the central and south Pacific Ocean. Temperature records at Fort Point, San Francisco indicate a seasonal minimum of 10.6°C, a mean of 13.0°C, and a maximum of 15.8°C. The species has not been collected at Fort Point but has been collected at Berkeley Yacht harbor not far from there in company with *L. (L.) quadripunctata*. At Honolulu, a locality with temperatures approaching the upper limits tolerated by this species, the minimum is 24.3°C, the mean 26.1°C, and the maximum 27.8°C. On the Atlantic coast the species is found from New York harbor to the Caribbean and the Gulf of Mexico as far south as Panama. Again no upper temperature limit is evident. At the Battery in New York harbor the mean seasonal temperature shows a minimum of 1.8°C, a mean of 12.2°C, and a maximum of 22.8°C. At Cristobal in the Canal Zone of Panama the mean seasonal temperatures are at a minimum 26.8°C, at a mean of 28.0°C, and at a maximum of 28.8°C.

Tropical Species

In addition to *L. (L.) tripunctata* five species appear to fall in this category; *L. (L.) simulata, L. (L.) platycauda, L. (L.) pfefferi, L. (L.) saseboensis,* and *Paralimnoria andrewsi*. Two of the latter species of *Limnoria* have been collected at Miami but not elsewhere and the others occur in the Caribbean area but have not yet been reported from Miami or other parts of Florida. Obviously the data are too scarce to permit a delineation of the natural temperature requirements. It is doubtful, however, that they will be found much north of Miami on the Atlantic coast or north of Mazatlan on the Pacific coast where many collections have failed to reveal their presence. Presumably the temperature characteristics of these areas are too low and variable to allow their occurrence. If Miami is in fact the northernmost limit for these species, then the optimal conditions might be found in temperature ranges somewhere between those of Miami

and the Caribbean areas. The seasonal temperature range at Miami has a minimum of 21.2°C, a mean of 25.6°C, and a maximum of 30.0°C. *Paralimnoria* also occurs in Honolulu where the seasonal averages are 24.3°C at minimum, 26.1°C at a mean and 27.8°C at a maximum.

Summary

1) The systematics, geographical distribution and ecology of the wood and seaweed boring marine isopods of the family Limnoriidae occurring in North and Central America are described.

2) A brief review of the literature concerning taxonomic, distributional, ecologic, physiologic, and anatomical studies is given.

3) Directions are given for the collection, preservation, and examination of *Limnoria* for study.

The storage of specimens in 75% ethyl alcohol is recommended as the most satisfactory means of preservation.

4) The general morphology of *Limnoria* is described and characteristics having taxonomic utility are discussed.

5) A comparison of *Limnoria* with the related isopods *Sphaeroma, Cirolana,* and *Cymothoa* leads to the suggestion that *Limnoria* should be placed in a distinct family the *Limnoriidae* Harger (emend.).

6) The family Limnoriidae is characterized and a key is given to the genera it contains. The following genera and subgenera are recognized: genus *Limnoria* (sensu lato) (type *Cymothoa lignorum* Rathke), subgenus *Limnoria,* subgenus *Phycolimnoria n.* subg., (type *P. algarum* n. sp.), genus *Paralimnoria* n. gen. (type *Limnoria andrewsi* Calman).

7) A key is given to the various species occurring in the Americas. The following are described:

Species	Type Locality
Limnoria (Limnoria) lignorum (Rathke)	Norway
Limnoria (Limnoria) quadripunctata Holthuis	Holland
Limnoria (Limnoria) pfefferi Stebbing	Minikoi Atoll, Indian Ocean
Limnoria (Limnoria) tripunctata Menzies	San Diego, California
Limnoria (Limnoria) platycauda n. sp.	Curacao, Dutch West Indies
Limnoria (Limnoria) saseboensis n. sp.	Sasebo, Japan

Limnoria (Limnoria) simulata n. sp.	Virgin Islands, West Indies
Limnoria (Phycolimnoria) algarum n. sp.	Dillon Beach, California
Paralimnoria andrewsi (Calman), forma typica	Christmas Island, Indian Ocean
Paralimnoria andrewsi (Calman), forma A	Curacao, Dutch West Indies
Paralimnoria andrewsi (Calman), forma B	Key West, Florida

8) Four species have been found on the Pacific coast; *L. (L.) lignorum, L. (L.) quadripunctata, L. (L.) tripunctata, L. (P.) algarum.*

Four species have been found on the Atlantic coast, (excluding the Gulf and Caribbean); *L. (L.) lignorum, L. (L.) tripunctata, L. (L.) pfefferi, L. (L.) saseboensis.*

Four species are known from the Caribbean Sea and Gulf of Mexico: *L. (L.) tripunctata, L. (L.) platycauda, L. (L.) simulata,* and *P. andrewsi.*

Two species are common to both coasts; *L. (L.) lignorum* and *L. (L.) tripunctata* with the latter species occurring in the Gulf and Caribbean as well.

9) The following environmental factors are suspected or known to influence the distribution of *Limnoria:* Food supply, depth and associated phenomena, dissolved oxygen content, salinity, and temperature. Each factor is discussed and examples of the influence of each on distribution are given where possible.

An average dissolved oxygen concentration below 1.4 ppm (between 1.6 and 0.12) appears to limit the animals. Salinities below 10% similarly seem limiting. Temperature appears to be the major factor associated with the distribution of the various species. Low temperatures adversely affecting the reproductive capacity of the animals are considerably higher than those lethal to the adults. Temperature is believed to limit the distribution of the species primarily through its influence on the animal's reproductive abilities.

10) The absence of *L. (L.) quadripunctata* from the Atlantic coast is postulated as being due to its having a stenothermic reproductive range. Temperatures suspected to be entirely favorable for its development on the Pacific coast were found to occur only two successive months out of the year at locations on the Atlantic coast from Boston to Charleston, S.C. On the other hand, they occurred 6-11

successive months out of the year at localities within the range of the species on the Pacific coast.

11) No truly *Arctic* species was found. Of the wood-borers *L. (L.) lignorum* shows a typical *boreal* distribution on both sides of America. *L. (L.) quadripunctata* shows a *temperate* distribution. One species, *L. (L.) tripunctata,* shows a *temperate-tropical* distribution and is found on both coasts. The remaining species show a *tropical* distribution.

TABLE 2.

MONTHS DURING THE YEAR THAT TEMPERATURES BETWEEN 11.4°C AND 16.2°C PREVAIL AT VARIOUS LOCALITIES ALONG THE PACIFIC AND ATLANTIC COASTS. LOCALITIES HAVING THE SPECIES *L. (L.) quadripunctata* ARE MARKED WITH AN ASTERISK.

LOCATION	MONTH												Total No. Months
	J	F	M	A	M	J	J	A	S	O	N	D	
PACIFIC													
Sitka, Alaska	0	0	0	0	0	+	+	+	+	0	0	0	4
Crescent City*	0	0	0	0	+	+	+	+	+	+	0	0	6
San Francisco*	0	+	+	+	+	+	+	+	+	+	+	+	11
Los Angeles*	+	+	+	+	+	0	0	0	0	0	+	+	7
Honolulu, T. H.	0	0	0	0	0	0	0	0	0	0	0	0	0
ATLANTIC													
Eastport, Me.	0	0	0	0	0	0	0	0	+	0	0	0	1
Boston, Mass.	0	0	0	0	+	+	0	0	0	+	0	0	3
New York, N.Y.	0	0	0	0	+	0	0	0	0	+	+	0	3
Charleston, S.C.	0	+	+	0	0	0	0	0	0	0	0	+	3
Port Isabel, Tex.	0	0	0	0	0	0	0	0	0	0	0	0	0
Miami, Fla.	0	0	0	0	0	0	0	0	0	0	0	0	0

PART II:
ADDITIONS TO THE SYSTEMATICS

INTRODUCTION

The general features of classification, methods of collection, identification, anatomy, and nomenclature have been presented in Part I. Here it is my purpose to accomplish four things: first, to provide redescriptions of the known species in the four cases where such are needed, and second, to give descriptions to eight additional new species of *Limnoria,* four of which belong to the subgenus *Phycolimnoria* and five to the subgenus *Limnoria,* which have been subsequently discovered in the course of my studies on *Limnoria.* The third objective is to present a discussion of various taxonomic monstrosities

which have arisen in the course of time since 1813 (1814) when Leach first gave the genus its present name. Finally a list has been compiled of the known and currently valid species with reference to their first description and subsequent revision.

Descriptions of Wood-borers

Redescriptions

Limnoria (L.) japonica Richardson
Figures 27-28

Synonymy:

Limnoria japonica Richardson, 1909, pp. 95-96, fig. 21. — Barnard, K. H., 1936, pp. 176-177.—Chilton, 1914a, pp. 382-387.—Kofoid and Miller, 1927, p. 309.—Holthuis, 1949, pp. 170-171.—Moll, 1915, p. 185, fig. 9.—Shiino, 1944, p. 2;—1950, p. 334.

Diagnosis. Flagellum of second antenna with four articles. Epipod of maxilliped not reaching the articulation of first article of palp with endopod; epipod semi-triangulate in shape, widest near the base and narrowing distally to a blunt point, length not exceeding three times the width. Mandibular palp with three articles. Fifth somite of pleon with two medially located tubercles, anterior tubercle separated from posterior one by a prominent sulcus. Pleotelson with a single prominent anterior medially located tubercle followed by a pair of large tubercles and their accompanying carinae. Posterior edge of pleotelson lacks tubercles and spike-like setae; lateral crests lack tubercles but have numerous spike-like setae. Lacinioid seta of right mandible with (usually) four distally spinulate branches near apex.

Measurements. Figured male paratype length 5.0 mm, pleotelsonal width 1.5 mm. Large ovigenous female paratype length 7.0 mm, telson width 1.7 mm. This species is evidently one of the largest of the genus, being excelled in size only by *L. (P.) stephenseni* n. sp. (p. 189).

Type locality. The types were taken from a depth of 163 fathoms at Lat. 37° 23′ N; Long. 137° 36′ E by the U. S. Fish Commission Steamer "Albatross" on the way from Nanoa, Hondo, Japan, to Isuruga, Hondo, Japan at Suduz Misaki Light (Richardson, 1909). The types are located in the U.S. National Museum, Cat. No. 39507.

Habitat. The types were taken from a water-logged fragment of bamboo.

Specimens examined. Over 30 cotypes were kindly sent to the writer by Dr. Fenner A. Chace, Jr., Curator, Marine Invertebrates, U. S. National Museum.

Geographical distribution. Known only from the type locality.

Remarks. Richardson's original description is erroneous in a number

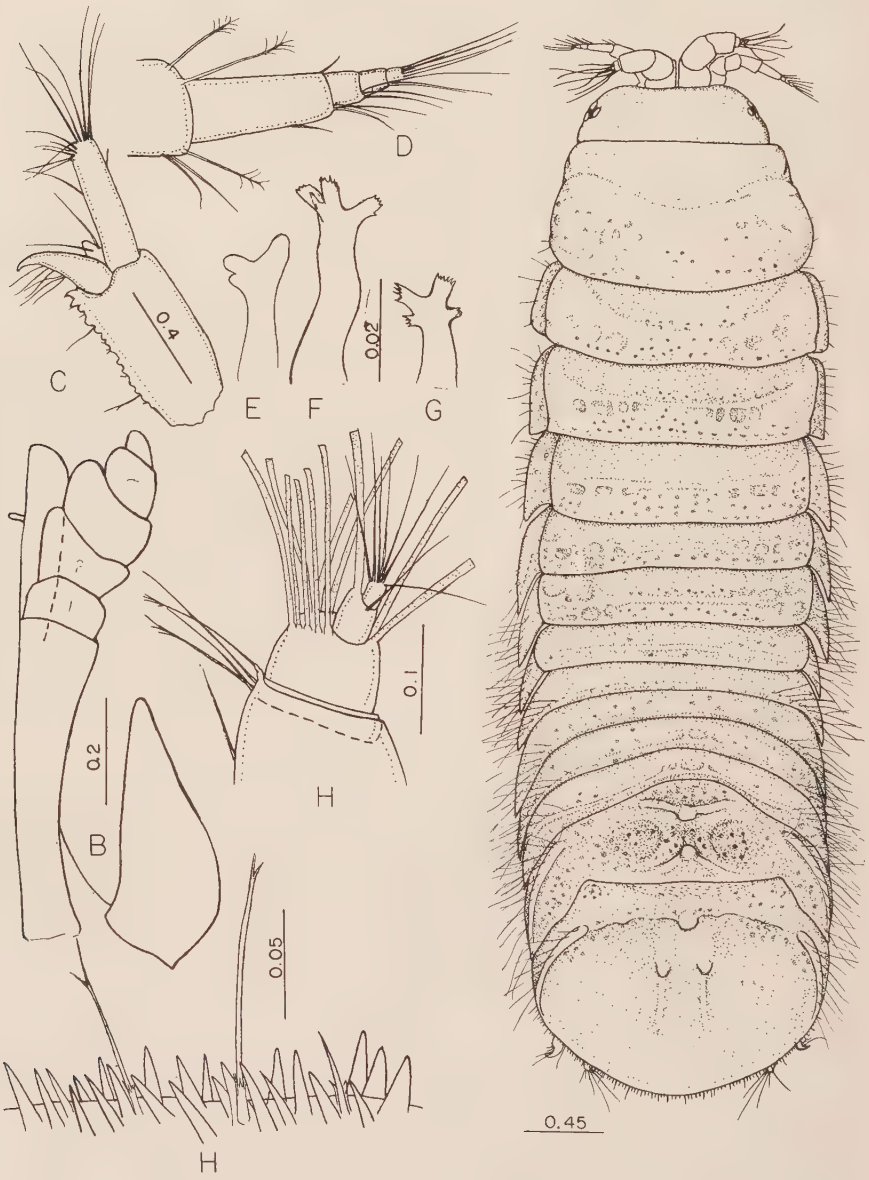

FIGURE 27. *Limnoria (L.) japonica* Richardson, cotype, male. A, lateral crest of pleotelson. B, maxilliped, setae omitted. C, uropod. D, flagellum of second antenna. E-G, lacinioid setae of right mandible. H, distal articles of first antenna. I, male. Figures with similar magnification, A; B, C; D, H; E, F, G; I.

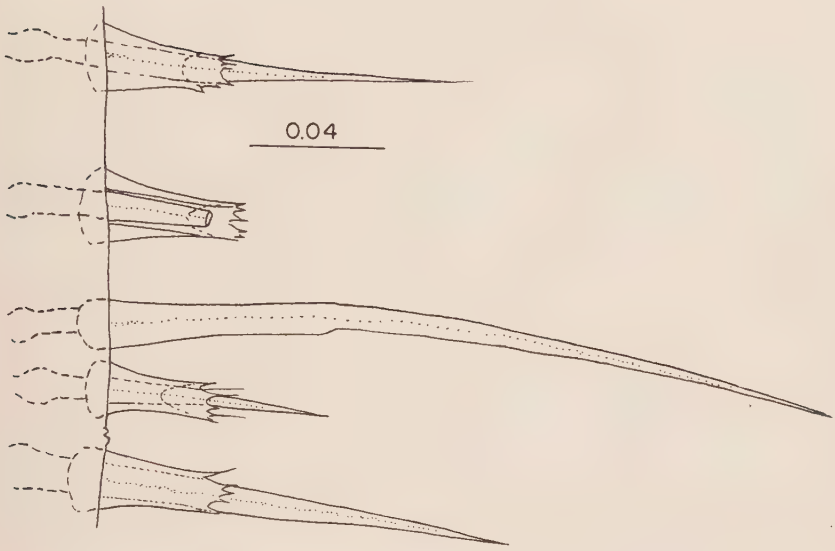

FIGURE 28. Pleotelsonic border of *L. (L.) japonica* Richardson.

of important respects. Most of these errors are corrected in the above diagnosis and therefore only a few additional notes need be given here. The first antenna consists of seven and not four articles. The flagellum of the second antenna has four and not five articles. Richardson did not mention the structure of the mandibles in her description and it is only by chance that Chilton (1914a, pp. 387-388) was correct when he assumed "that its mandible (palp) will be found to be three jointed and the epipods of the maxilliped to be short". Chilton in apparent disregard of this assumption however places *L. (L.) japonica* in his key with the species having "epipod of maxilliped longer than second joint". Holthuis (1949, p. 170) placed *L. (L.) japonica* in the group having the epipod of the maxilliped shorter than the second joint of the maxilliped, yet he, like the rest, had not seen specimens of *L. (L.) japonica*. Shiino (1944 and 1950) considered *L. (L.) japonica* a synonym of *L. (L.) tripunctata* (called *L. (L.) lignorum* by Shiino) and while the three tubercles on the pleotelson are similar to those of *L. (L.) tripunctata* the ornamentation of the fifth pleonal somite is different and the flagellum of the second antenna has four and not five articles and the pleotelsonal margin lacks the tuberculations characteristic of *L. (L.) tripunctata*.

Limnoria (?L.) septima Barnard

Figure 29

Synonymy:

Limnoria septima Barnard, 1936, pp. 174-177, text-figs. 11-12. — Holthuis, 1949, pp. 170-171.

Diagnosis. Flagellum of second antenna with five articles. Epipod of maxilliped not reaching the articulation of the first article of the palp with endopod; epipod semi-triangulate, narrowing distally to a point, and widest at base; length about three times the width. Mandibular palp with three articles. Structure of mandibular incisor not known. Fifth somite of pleon medially with a distal horseshoe-shaped carina and an opposing proximal horseshoe-shaped carina between which is an unornamented sulcus. Pleotelson with a medial elevated, bituberculate horseshoeshaped carina distal to which are two parallel carinae. Posterior margin of pleotelson with a dorsally directed fringe of spike-like setae, marginal setae numerous, tuberculations absent. Lateral crests devoid of tubercles. Structure of lacinioid seta of right mandible not known.

Measurements. Figured female cotype, length 6.4 mm, width of pleotelson 1.7 mm Barnard (1936) records the female cotypes as being 5.25 mm and 5.75 mm in length. Because he had only two adult female specimens the one examined by me should be one of them. There exists, therefore, a minimal difference of 0.65 mm. between the measurements. This may be due to a separation of the somites of the specimen and the resultant stretching of the body.

Type locality. The types were taken from a depth of between 185 and 250 fathoms in the Indian Ocean by the R.I.M.S. "Investigator" at two localities, North Sentinel, Andamans, 3 specimens, and Station 233, 13° 17′ 15″ N by 93° 10′ 25″ E, at 185 fathoms, Andamans. 1 juv. specimen (Barnard, 1936).

Habitat. No indication was given by Barnard as to the habitat of this species. In the absence of such information, three possibilities suggest themselves: (1) the specimens were taken from floating seaweed which was incidentally taken in the dredge haul; (2) they were taken from water-logged wood; (3) or they were taken free in the dredge haul in association with neither algae nor wood. The third possibility seems unlikely in view of the boring habits of the species of *Limnoria*. The others could be decided by a removal of the mandibles or an examination of the gut contents. Dissection of the cotype seemed inadvisable because the mandible were not movable without possible injury of the specimen. The food of this species and hence its subgeneric assignment will probably have to await the collection of more material.

Specimens examined. One female cotype was examined. This was

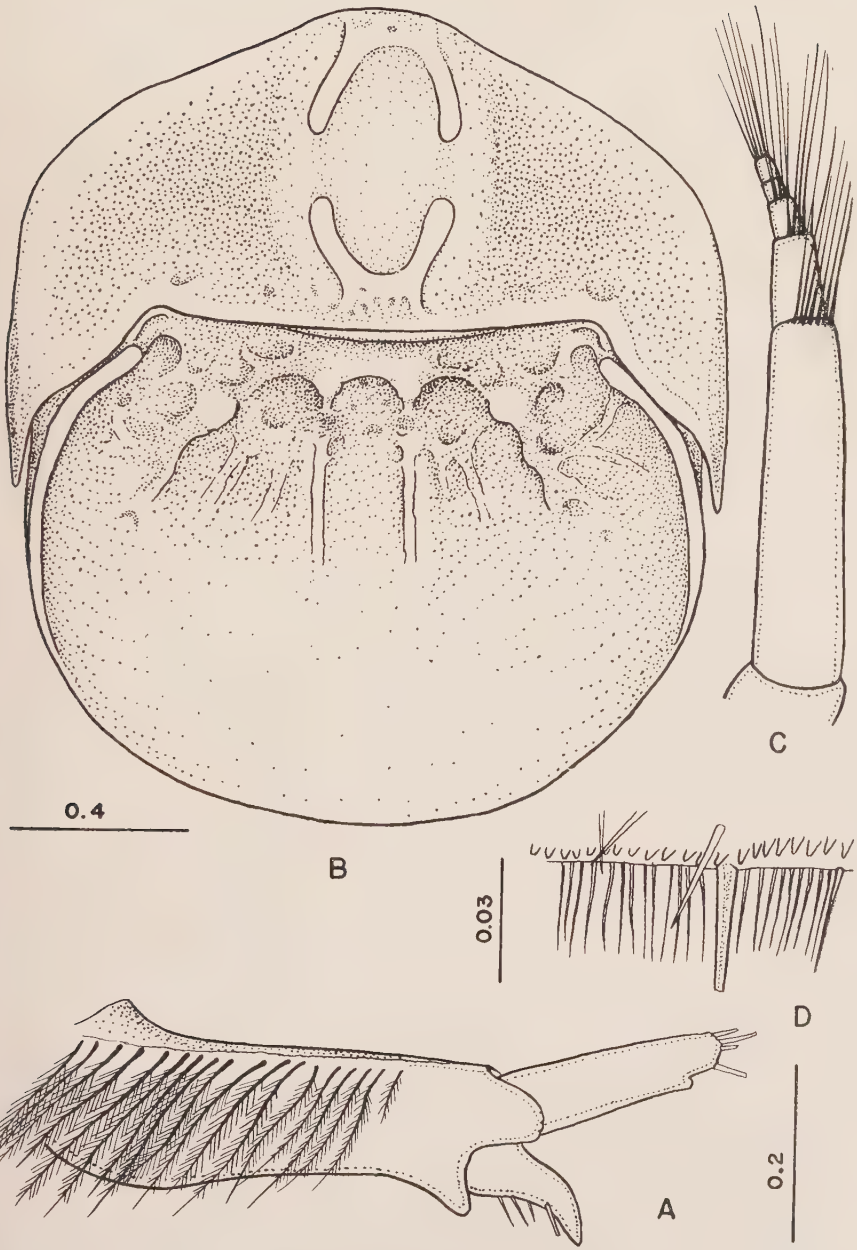

FIGURE 29. *Limnoria (?L.) septima* Barnard, female cotype. A, uropod. B, pleotelson. C, flagellum of second antenna. D, posterior edge of pleotelson. Figures with similar magnification, A, C; B; D.

very kindly sent as a loan to the writer by Dr. K. K. Tiwari, Carcinologist, Zool. Survey India, Calcutta, India.

Geographical distribution. Known only from the type locality.

Remarks. The description given this species by Dr. Barnard (1936) is in general very good; however, a few points need correction. The most anterior carina of the fifth somite of the pleon is horse-shoe shaped and not only a pair of parallel ridges as Barnard describes and figures. The second antenna is not "as in *lignorum*" because its flagellum consists of five and not four articles. Each maxilliped has one coupling hook which was not mentioned by Barnard. The maxillipedal epipod is not nearly as short as that figured by Barnard but extends at least three-fourths the length of the "end joint". Barnard (1936, p. 176) states that his specimens "bear most resemblance" to *L. (L.) japonica.* This is not the case because *L. (L.) japonica* belongs to the group of *Limnoria* characterized by having a second antennal flagellum with four and not five articles and an anterior medially located tubercle on the pleotelson.

Holthuis (1949, p. 171) thought that *L. (L.) quadripunctata* and *L. (L.) septima* were closely related because they resembled each other in the shape of the uropods. This is not the case because, as Barnard remarks, "the inner ramus is only one-half the length of the peduncle," whereas in *L. (L.) quadripunctata* Holthuis, the inner ramus (endopod) is, as Holthuis figures (Holthuis, 1949, fig. 2i), about equal to the length of the peduncle.

New Species

Limnoria (L.) multipunctata, new species

Figures 30-31

Diagnosis. Flagellum of second antenna with four articles. Epipod of maxilliped reaching slightly beyond articulation of first article of palp with endopod; epipod spatulate in shape, blunt at distal end, being two and three-quarters times as long as wide. Mandibular palp with three articles. Fifth somite of pleon smooth medially. Pleotelson medially with an anteriorly located pair of tubercles followed by a larger more posteriorly located pair. This is followed by a multituberculate medially located carina. Posterior border of pleotelson with a conspicuous fringe of tubercles, spike-like setae lacking; lateral crests tuberculate. Lacinioid seta of right mandible reduced, simple, lacking spinules or serrations.

Measurements. Holotype male length, 1.9 mm; pleotelson width 0.4 mm. Allotype length, 2.0 mm; pleotelson width 0.4 mm.

Type locality. The type specimens were taken off the Kai Islands (5°-6° 5′ S by 131° 5′ to 133° 15′ E) in the South Pacific Ocean

FIGURE 30. *Limnoria (L.) multipunctata,* new species, male paratype. A, male. B, lateral crest of pleotelson. C, lateral margin of peraeon. D, distal articles of uropod (endopod not figured). E, distal articles of first peraeopod. F, maxilliped. Figures with similar magnification, A, C; B, D, E, F.

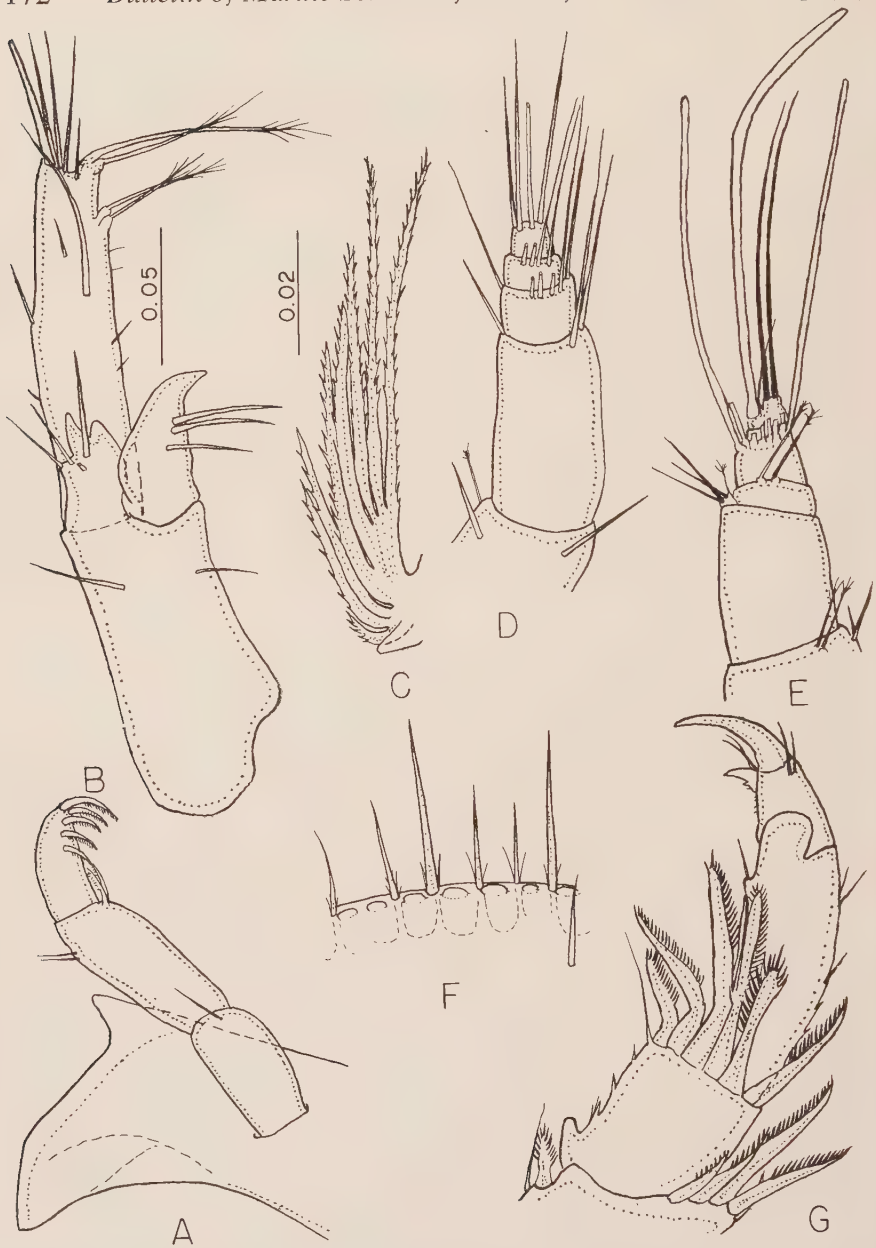

FIGURE 31. *Limnoria (L.) multipunctata,* new species, male paratype. A, mandible. B, uropod. C, setal row and lacinioid seta of right mandible. D, flagellum of second antenna. E, flagellum of first antenna. F, posterior edge of pleotelson. G, distal articles of seventh peraeopod. Figures with similar magnification, A, B, D, E, G; C; F.

from a depth of 13 meters on June 12, 1922, by the Danish Expedition to Kei-Oerne (Kai Isls.) in 1922. The specimens were lent to me by Dr. Torben Wolff, of the Universitetets Zoologiske Museum, Kϕbenhavn. The types consisting of a holotype, allotype and 55 paratypes have been returned to that institution. Five paratypes have been deposited in the collections of the United States National Museum, Washington, D. C.

Habitat. The specimens were removed from their burrows on a piece of *Teredo* infested wood.

Specimens examined. Other than the above mentioned types, specimens were examined which had been collected from the following localities in the Pacific Ocean. *Saipan Island,* U. S. Navy, July, 1948, 6 specimens, Charles H. Edmondson collection. *Canton Island,* Phoenix Isls., U. S. Navy, 1948-49 (?), 9 specimens, C. H. Edmondson collection. *Guam Island,* K. V. Bossler, July 30, 1946, 14 specimens, C. H. Edmondson collection. The specimens from Saipan were found in wood which was also attacked by *L. (L.) tripunctata* and *Paralimnoria andrewsi.*

Geographical distribution. South and Central Pacific Ocean at Guam, Saipan, Canton Isl., and the Kai Isls.

Remarks. The species appears similar to *L. (L.) platycauda* Menzies (p. 139), but differs markedly from the species in the tuberculations of the pleotelson and in the absence of a mid-longitudinal carina on the fifth somite of the pleon.

Limnoria (L.) unicornis, new species
Figure 32

Diagnosis. Flagellum of second antenna with four articles. Epipod of maxilliped short, not reaching the articulation of first article of palp with endopod; semi-triangulate in shape, three times as long as wide; apex acute. Mandibular palp with one article. Fifth somite of pleon with an anteriorly located, depressed, triangulate area on mid-line followed by a mid-longitudinal carina. Pleotelson with a large, elevated, median tubercle at proximal end. Posterior margin of pleotelson lacking tubercles; spike-like setae present. Lateral crests lack tubercles. Lacinioid seta of right mandible a simple, apically spinulate seta.

Measurement. Holotype male, length 2.9 mm, width of pleotelson 0.65 mm.

Type locality. Ponape, Caroline Isls., Pacific Ocean, 1948 (?), collected by U. S. Navy for C. H. Edmondson, holotype male, plus one pleon. These have been returned to Dr. Edmondson. In the vial with

FIGURE 32. *Limnoria (L.) unicornis,* new species, male holotype. A, posterior edge of pleotelson. B, maxilliped. C, flagellum of second antenna. D, accessory claw of first peraeopod. E, uropod. F, lacinioid seta of right mandible. G, pleotelson. H, right mandible, outer surface. I, lateral crest of pleotelson. Figures with similar magnification, A, D, H, I; B, C, E; G; F (magnification not known).

this species were some specimens of *L. (L.) insulae* (p. 178).

Habitat. From wooden test sample.

Specimens examined. Types only.

Geographical distribution. Known only from Ponape Isl.

Remarks. This species is unique in having a mandibular palp consisting of only one article. In pleotelsonal ornamentation this species resembles the algal borers *L. (P.) segnis* (Chilton) and *L. (P.) segnoides* Menzies (p. 184) which species similarly exhibit a reduction in the number of articles of the mandibular palp.

Limnoria (L.) foveolata, new species
Figure 33

Diagnosis. Flagellum of second antenna with five articles. Epipod of maxilliped just reaching the articulation of palp with endopod. Epipod strap-like but tapering gradually to a point at distal end, being three times as long as wide. Mandibular palp with three articles. Fifth somite of pleon foveolate, central portion raised and provided with deep pits and subparallel irregular ridges. Pleotelson medially with two tubercles at anterior end each followed by an irregular carina; lateral areas deeply foveolate. Posterior edge of pleotelson lacking tubercles and regularly arranged spike-like setae which are minute and delicate. Lateral crests of pleotelson devoid of tubercles. Lacinioid seta of right mandible with three medially recurved spines at apex.

Measurements. Holotype female, length 2.2 mm, width of pleotelson 0.5 mm.

Type locality. The holotype, and only specimen, was collected at Station 103 of the Danish Expedition to the Kei-Oerne (Kai Islands) in 1922 from a depth of 52 meters in the Sigsbee trawl. The specimen has been returned to Dr. Torben Wolff of the Universitetets Zoologiske Museum, Kφbenhavn.

Habitat. Nothing was given on the label which might indicate from which material the specimen was taken. From the structure of the mandibles a wood-boring habit is clearly indicated.

Specimens examined. Type only.

Geographical distribution. Known only from the type locality.

Remarks. Superficially this species resembles *L. (L.) saseboensis* Menzies (p. 141) to a considerable degree. It can be distinguished from it by the lack of marginal tubercles on the pleotelson and by its much longer maxillipedal epipod.

Limnoria (L.) sublittorale, new species
Figure 34

Diagnosis. Flagellum of second antenna with five articles. Epipod of max-

illiped triangulate, elongated, reaching to the articulation of the first article of palp with endopod. Epipod three times as long as wide. Mandibular palp with three articles. Fifth somite of pleotelson with a pair of longitudinal carinae mid-dorsally. Pleotelson with a pair of parallel longitudinal carinae mid-dorsally; posterior margin with a fringe of upward-directed spike-like setae and a margin of simple setae of differing lengths. Lacinioid seta of right mandible with two recurved teeth at apex.

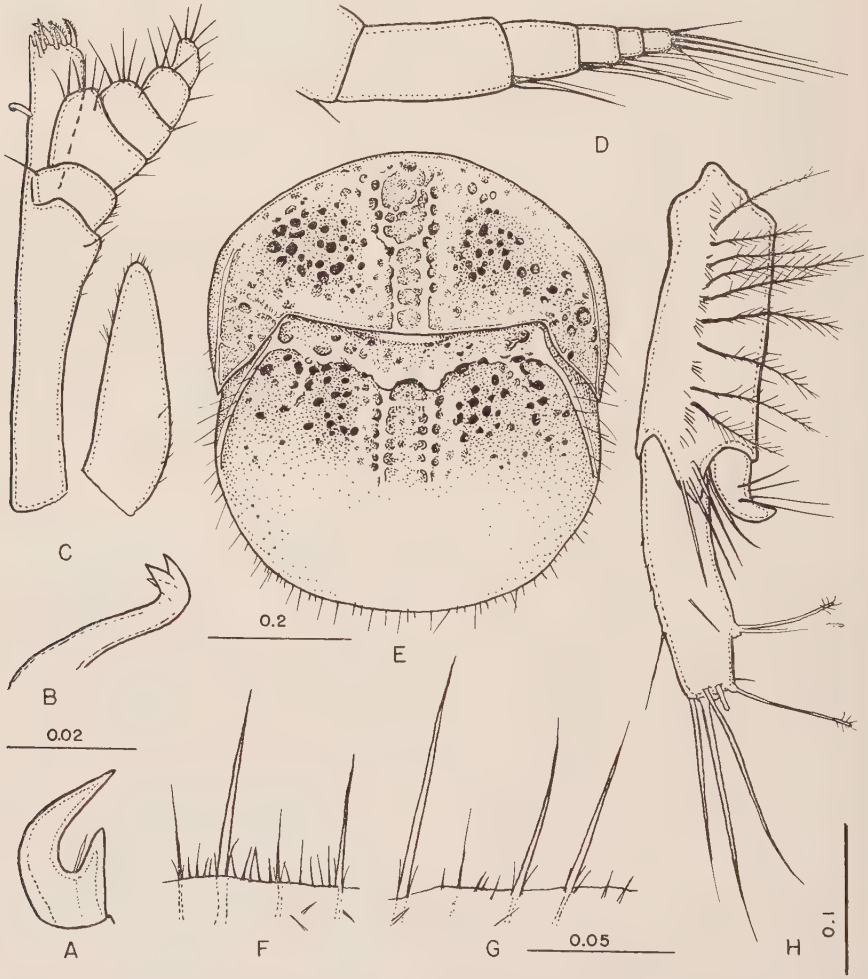

FIGURE 33. *Limnoria (L.) foveolata,* new species, holotype. A, accessory claw of first peraeopod. B, lacinioid seta of right mandible. C, maxilliped. D, flagellum of second antenna. E, pleotelson. F, uropod. G, posterior margin of pleotelson. H, lateral crest of pleotelson. Figures with similar magnification, B; D, H; E; F, G; A and C not known.

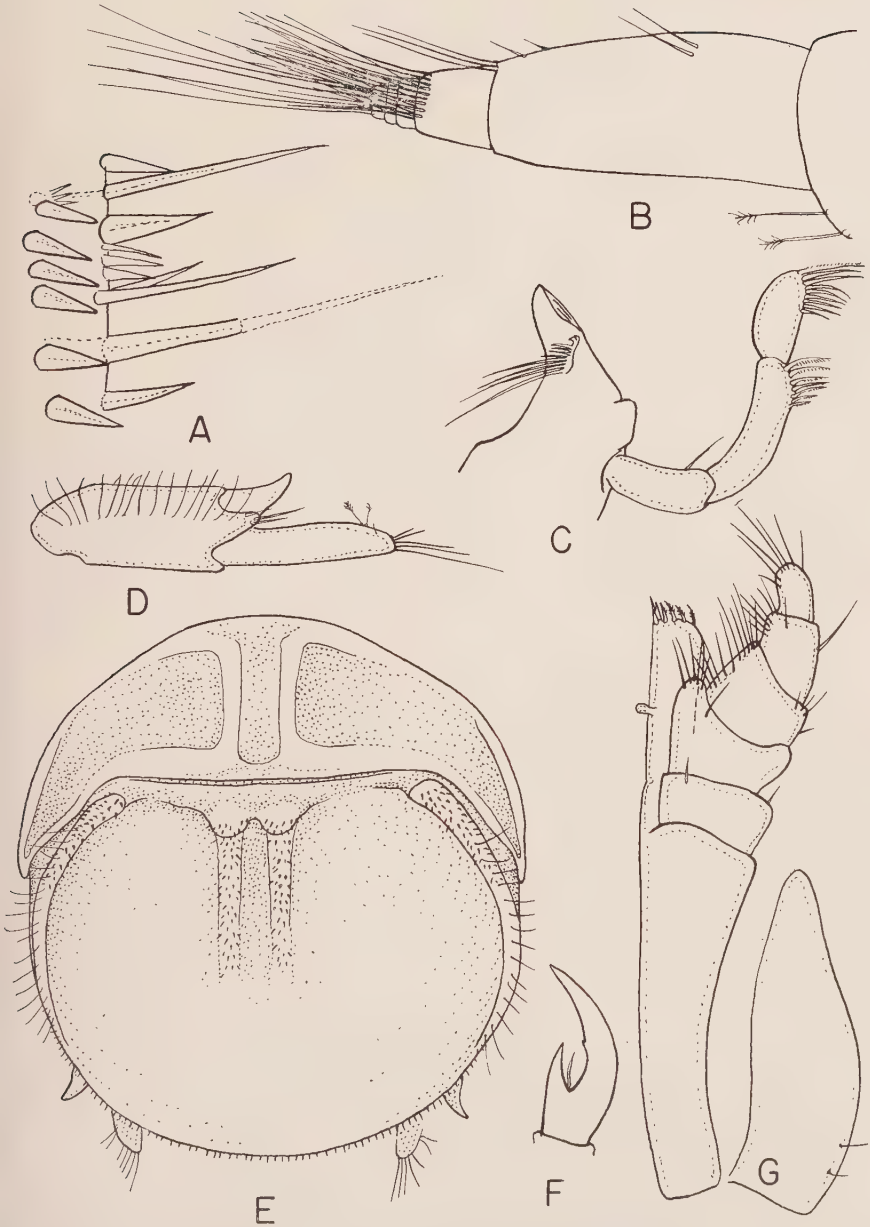

FIGURE 34. *Limnoria (L.) sublittorale*, new species, male paratype. A, posterior border of pleotelson. B, flagellum of second antenna. C, right mandible. D, uropod. E, pleotelson. F, accessory claw of dactyl of first peraeopod. Magnification, scales various, all taken from paratype 4 mm in length and 1.2 mm in width of pleotelson.

Measurements. Holotype male, length 5.0 mm, width of pleotelson 1.3 mm. Paratype male, length 4.0 mm, width of pleotelson 1.2 mm.

Type locality. From Oregon fir (Douglas fir) timber forming part of the frame of Otter board of Otter fish trawl retrieved from 60 fathoms off the coast of New South Wales, Australia. Collected by Frank McNeill, Australian Museum, Sydney, N.S.W., Australia. The specimens have been returned to Frank McNeill.

Specimens examined. Types only.

Geographical distribution. Known only from type locality.

Remarks. This species resembles *Limnoria (L.) quadripunctata* Holthuis and especially *L. (L.) saseboensis* Menzies (p. 141). It differs from *quadripunctata* in the structure of the carinae on the fifth somite of the pleon and from *saseboensis* in lacking tuberculations along the posterior margin of the pleotelson. It differs from *L. (L.) foveolata* in having a fringe of stout spike-like upward directed setae along the posterior margin of the pleotelson.

Limnoria (L.) insulae, new species
Figure 35

Diagnosis. Flagellum of second antenna with four articles. Epipod of maxilliped just reaching the articulation of first article of palp with endopod. Epipod spatulate, widest near middle, two and three-quarters times as long as wide. Mandibular palp with three articles. Fifth somite of pleon with a conspicuous hump on midline near distal border. In females the hump is markedly reduced to only a mid-longitudinal carina. Pleotelson lacking ornamentation but the lateral crests of the male particularly are much elevated and extend outward over the cup-shaped part of the pleotelson. Posterior margin of pleotelson tuberculate; spike-like setae lacking. Lacinioid seta of right mandible with two apical spines.

Measurements. Holotype male, length 3.8 mm, width of pleotelson 1.0 mm. Allotype length 3.0 mm, width of pleotelson 0.8 mm.

Type locality. Serua, Fiji Isl., December 15, 1952, low tide level, coconut tree trunk, 139 specimens collected by Dr. Martin W. Johnson. With this species were specimens of *L. (L.) tripunctata* Menzies and *L. (L.) saseboensis* Menzies.

Material examined. 137 paratypes from Fiji in addition to the holotype and allotype. *Guam Isl.,* one male, collected by K. V. Bossler, from C. H. Edmondson collection with specimens of *L. (L.) multipunctata* (p. 170). *Palmyra Isl.,* U.S. Navy, 2 specimens, collection of

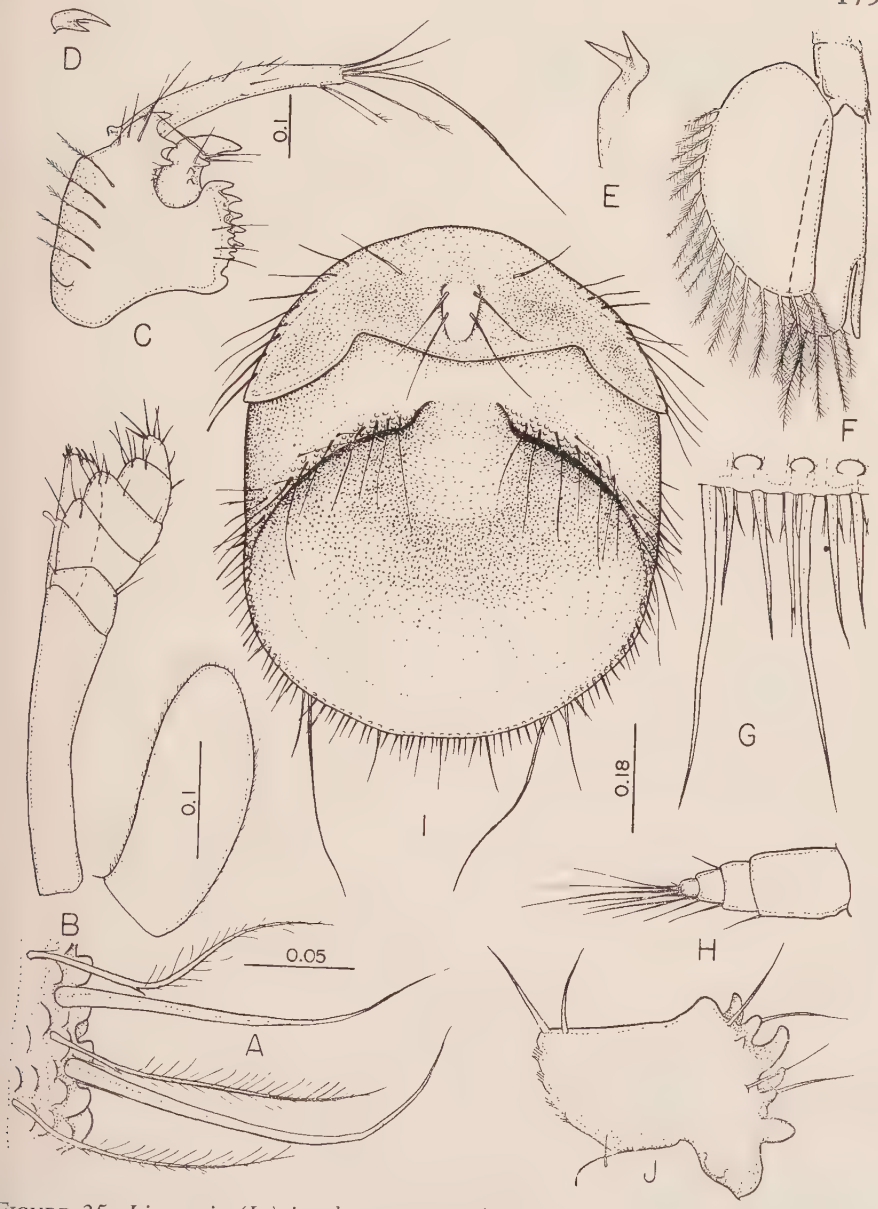

FIGURE 35. *Limnoria (L.) insulae,* new species, male. A, lateral crest of pleotelson. B, maxilliped. C, uropod. D, accessory claw of first peraeopod. E, acinioid seta of right mandible. F, second pleopod. G, posterior edge of pleotelson. H, flagellum of second antenna. I, pleotelson. J, merus of first peraeopod. Figures with similar magnification, A, D, G, H, J; B; C, F, I; E.

C. H. Edmondson. *Ponape*, Caroline Isls., U.S. Navy, one male, collection of C. H. Edmondson.

Geographical distribution. South Pacific Ocean.

Remarks. The peduncle of the uropods of this species are markedly compressed and the tuberculations are spine-like. This characteristic and the cup-like nature of the pleotelson distinguishes this species from all others known to date.

Descriptions of algal-borers

Redescriptions

Limnoria (Phycolimnoria) antarctica (Pfeffer)

Figure 36

Synonymy:

Limnoria antarctica Pfeffer, 1887, pp. 96-102, pl. 2, figs. 12-13, pl. 5, figs. 2-22; — 1890, p. 504. — Vanhöffen, 1914, pp. 509 510.

Diagnosis. Flagellum of second antenna with four articles. Epipod of maxilliped reaching slightly beyond the articulation of palp with endopod; epipod strap-like, slightly narrow at apex, slightly more than four times as long as wide. Fifth somite of pleon with a distinct transverse ovoid carina near distal margin and a pair of irregularly parallel carinae in the sulcus between them. Pleotelson medially with a large median swelling which is followed by a pair of parallel carinae; lateral to these are less distinct irregular carinae. Posterior margin of pleotelson with a dorsal fringe of large spike-like setae, margin with large distinctive setae. Entire pleotelson provided with distinct spike-like seta. Lateral crests devoid of tubercles. Lacinioid seta similar to other setae in setal row.

Measurements. Pfeffer (1887, p. 102) gives the length of one type as 4.5 mm, greatest width 1.6 mm. The longest specimen of the 58 type specimens examined by me was 5.0 mm in length.

Type locality. Süd-Georgian I., 1883, Ebbe unter Steinen, dieselbe Art ist in hohlen gangen in Tangwurzeln, No. K 19355, Hamburg Museum.

Habitat. This species was collected from algae under stones and from bore-holes in *Macrocystis* according to the label on the vials and from Pfeffer's (1887) description.

Specimens examined. A total of 58 type specimens were examined which were generously sent as a loan by Dr. A. Panning, Curator of Zoology, Hamburg Museum.

Geographical distribution. South Georgia Isl.—(Pfeffer, 1887), Kerguelen (Dreiinselhaven and Observatory Bay, Vanhöffen, 1914).

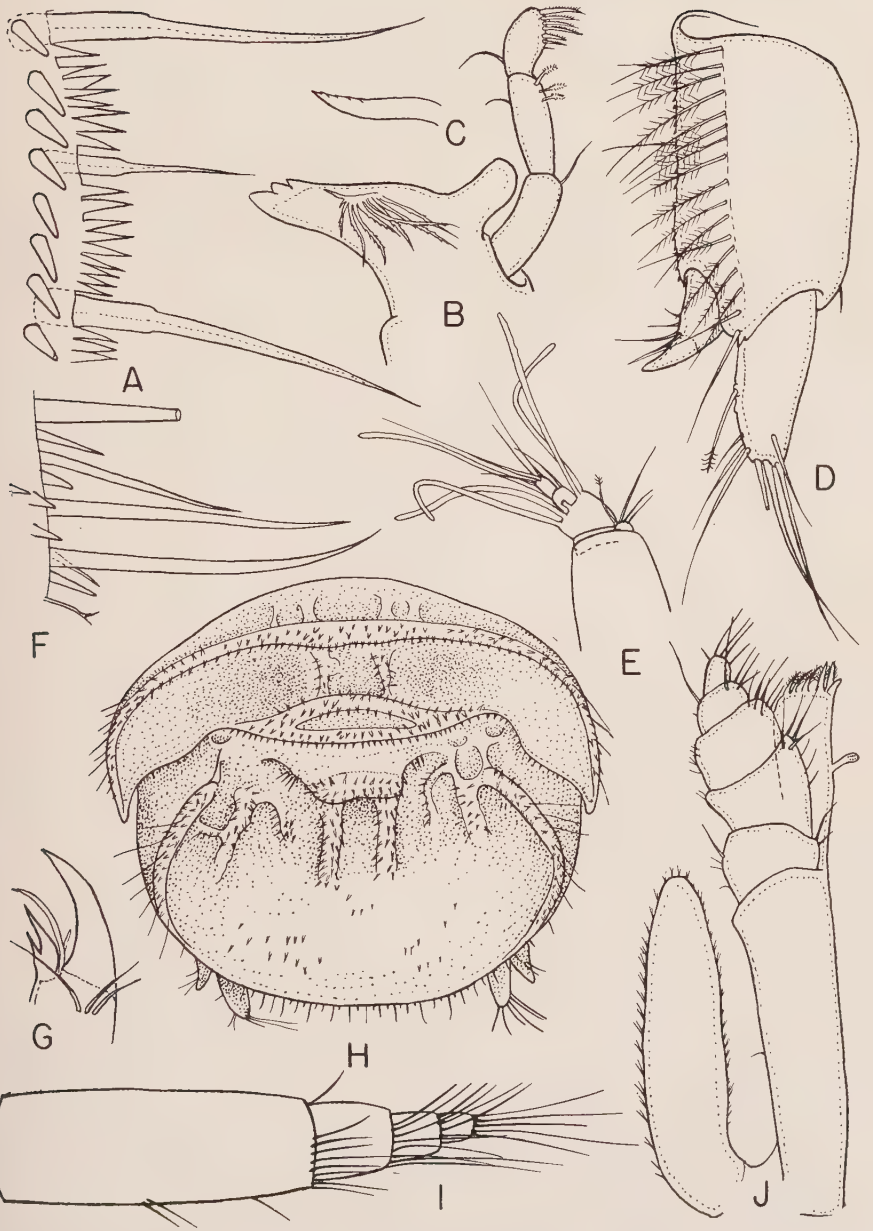

FIGURE 36. *Limnoria (P.) antarctica* (Pfeffer), cotype, ovigerous female. A, posterior border of pleotelson. B, right mandible. C, lacinioid seta of right mandible. D, uropod. E, flagellum of first antenna. F, lateral crest of pleotelson. G, dactyl of first peraeopod. H, pleotelson. I, flagellum of second antenna. J, maxilliped. Scales of magnification various, all appendages taken from ovigerous females of 5 mm length and 1 mm in pleotelsonal width.

Remarks. Pfeffer's elaborate description of this species is particularly good. The transverse carina on the fifth pleonal somite, a feature peculiar to this species, is shown by Pfeffer; however, the distinctive pleotelsonal carinae are only slightly indicated in the figures given by Pfeffer. The eyes have the usual seven facets and not only four. Pfeffer's figure of the uropod is incorrect because the exopod is claw-like and not a miniature of the endopod. Several of the illustrations given by Pfeffer are incorrect although they show the general form and proportions rather accurately.

It is doubtful that the specimens which Hale (1937) refers to this species actually belong to it. In the first place the mature specimens examined by Hale are twice the length of Pfeffer's specimens. Secondly, the uropodal exopod of *antarctica* is 2/3 the length of the endopod and not ½ the length of the endopod as it is in Hale's specimens. Hale's specimens have been referred to a new species, *L. (P.) stephenseni* which is described in this paper and which Stephensen had originally considered but with some doubt as equal to *Limnoria pfefferi* Stebbing. These specimens Hale considered as synonyms of *L. (P.) antarctica.*

It is now impossible, without examination of the specimens, to assign to a species the specimens which were reported by Richardson (1913) from the Deception and South Shetland Islands.

Limnoria (Phycolimnoria) segnis (Chilton)
Figure 37

Synonymy:

Limnoria segnis Chilton, 1883, pp. 76-77, pl. 2, fig. 1; 1914a, pp. 381-389, pl. XVII, figs. 1-5; — 1919, pp. 4-6, figs. 3, 5. — Kofoid and Miller, 1927, p. 309. — Holthuis, 1949, p. 170. — Moll, 1915, p. 184, fig. 6. — Stebbing, 1893, pp. 367-368; — 1905, p. 714.

Diagnosis. Flagellum of second antenna with three-four articles. Epipod of maxilliped reaching beyond the articulation of the first and second articles of the palp; epipod strap-like, elongated, being five times as long as wide. Mandibular palp with only two articles. Fifth somite of pleon with a median longitudinal carina which appears broken at the center, and anteriorly inconspicuously bifurcated. Pleotelson medio-anteriorly with a short transverse ridge having swollen tuberculiform areas at each end; each tuberculiform ridge followed distally by a short longitudinal ridge. Posterior edge of pleotelson lacks tubercles but bears a fringe of dorsally directed spike-like setae near the margin. Lacinioid seta of right mandible not markedly different from setae of setal row.

Measurements. Chilton (1883) remarks that the length of this species is one-sixth of an inch (about 4 mm). The largest cotype specimen

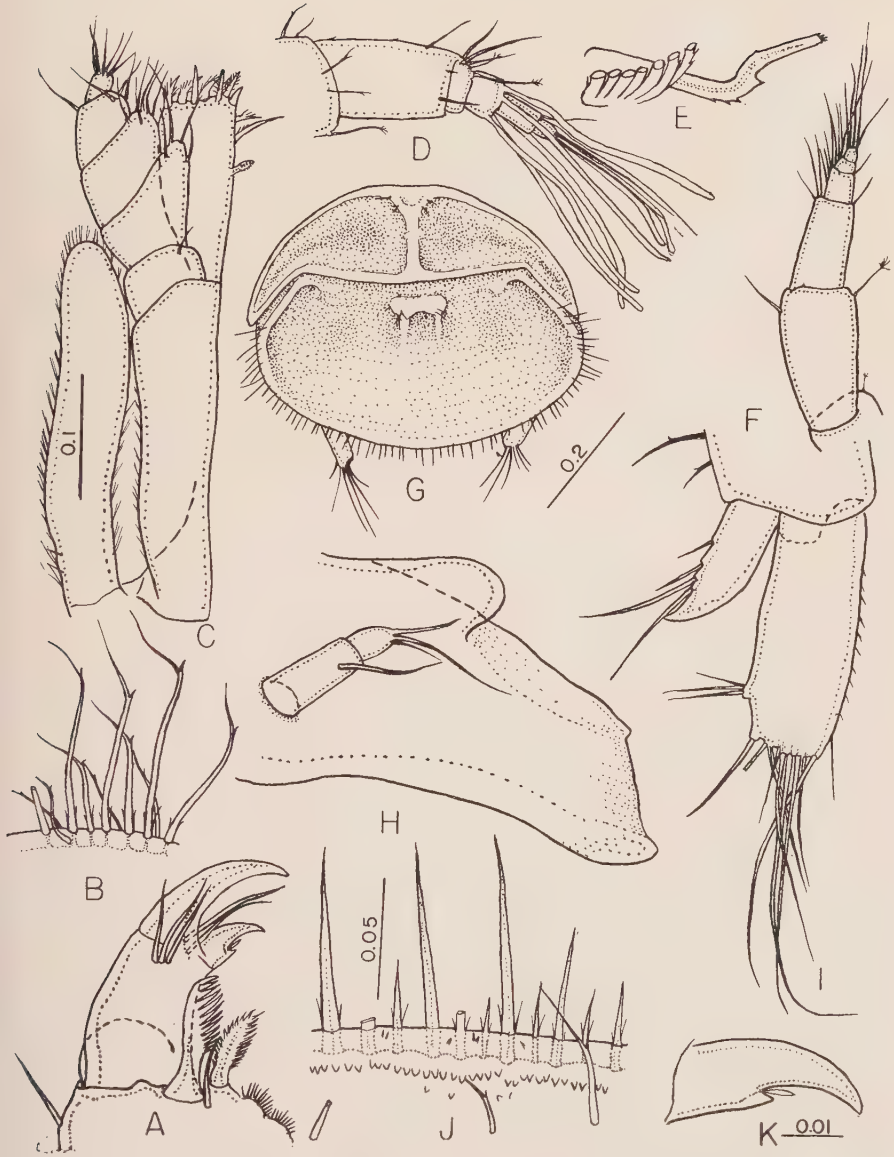

FIGURE 37. *Limnoria (P.) segnis* (Chilton), female, homoeotype. A, distal articles of first peraeopod. B, lateral crest of pleotelson. C, maxilliped. D, distal articles of first antenna. E, setal row and lacinioid seta of right mandible. F, apical articles, including flagellum, of second antenna. G, pleotelson. H, outer aspect of mandible. I, uropod. J, distal margin of pleotelson. K, accessory claw of first peraeopod. Figures with similar magnification, A, B, J, H; C, D, F, I; G; E, K.

examined by me was 4.0 mm in length and 1.0 mm in the width of the pleotelson.

Type locality. The species was originally taken "on seaweed" at Lyttelton Harbor, New Zealand (Chilton). Later Chilton (1914a, p. 382) notes that specimens were taken from holdfasts of *Macrocystis*. The types are located in Dr. Chilton's collection at Canterbury University College, Christchurch, New Zealand.

Specimens examined. Two lots of specimens were examined. Both were from Lyttelton Harbor and both were identified by Dr. Chilton. The first lot containing two ovigerous females and one male was sent to me by Dr. Isabella Gordon of the British Museum (Natural History). The second lot consisting of 14 cotype specimens was the loan of the Department of Biology, Canterbury University College, Christchurch, New Zealand, through the kindness of Dr. E. Percival, Professor of Biology.

Geographical distribution. The species thus far has been recorded only from Lyttelton and Akaroa Harbors, New Zealand (Chilton, 1914, p. 382).

Remarks. In the original description Chilton (1883) failed to record the sculpturing present on the dorsal surface of the fifth somite of the pleon and pleotelson. Later (1914, p. 383) he describes essentially what is shown in the figure reproduced here. His original figure of the maxilliped shows the palp consisting of only four articles. Later (1914a, pl. XVII, fig. 2) he indicates five articles; however in 1919 (fig. 5) he shows only four. In 1883 (fig. 1c) he shows a strap-like maxillipedal epipod; whereas in later papers he figures the epipod as club-shaped. The shape of the maxillipedal epipod is usually characteristic for each species; therefore, the possibility that Chilton confused two species should not be overlooked. The reduction of the mandibular palp from three to two articles is an interesting and useful specific characteristic. Chilton (op. cit.) was unable to find the scale of the first antenna, which is definitely present though concealed by an overgrowth of the preceding article of the antenna.

New Species

Limnoria (Phycolimnoria) segnoides, new species

Figure 38

Diagnosis. Flagellum of second antenna lost. Epipod of maxilliped clavate, widest at mid-region, being about three times as long as wide and extending

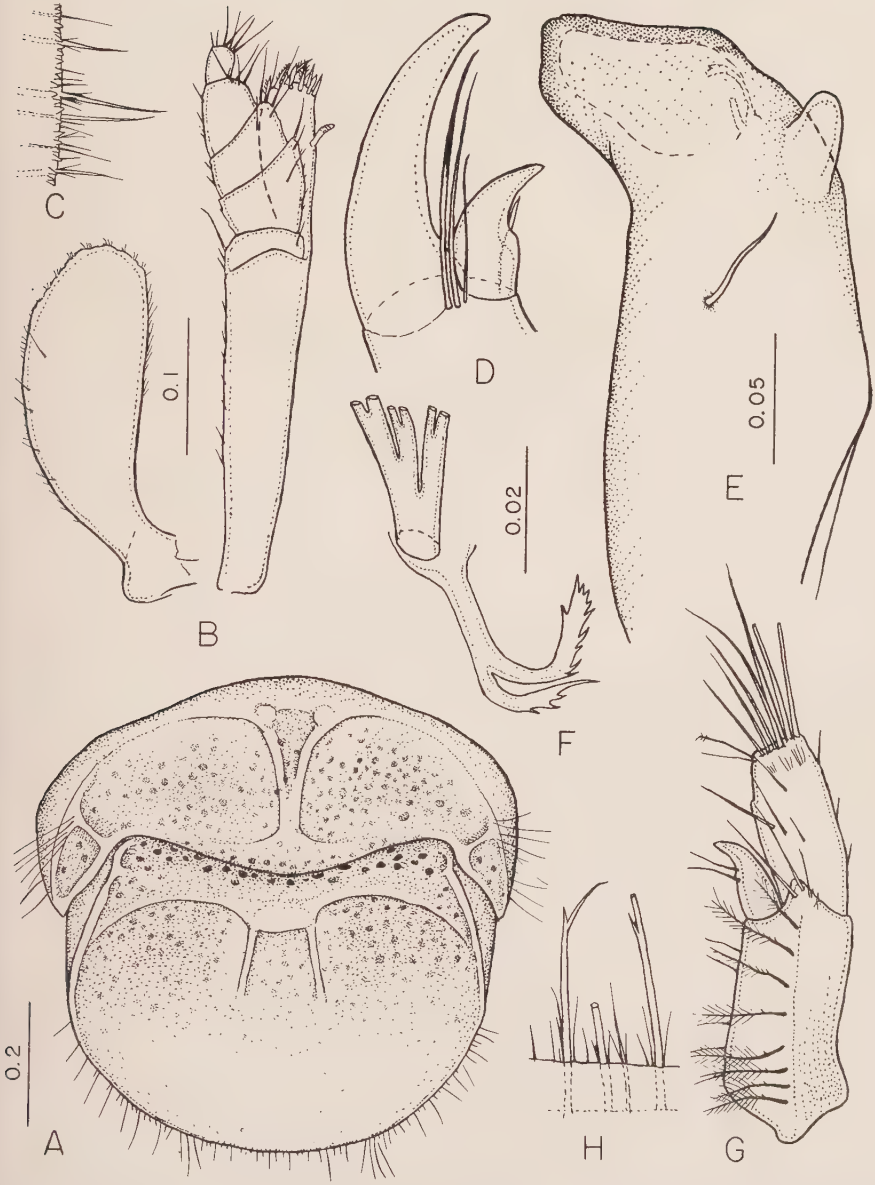

FIGURE 38. *Limnoria (P.) segnoides,* new species. A, pleotelson. B, maxilliped. C, posterior margin of pleotelson. D, distal parts of first peraeopod. E, outer surface of left mandible. F, lacinioid seta and setal row of right mandible. G, uropod. H, lateral crest of pleotelson. Figures with similar magnification, A; B, G; C, E, H; D, F.

to the articulation of palp with endopod. Mandibular palp lacking but is replaced by a stout long seta. Fifth somite of pleon with a median V-shaped carina. Pleotelson medially with an elevated anteriorly located region followed by two subparallel carinae. Posterior edge of pleotelson lacking tubercles but bearing a fringe of dorsally directed spike-like setae near margin. Lacinioid seta of right mandible composed of two simple marginally serrated setae which are similar to those in the setal row.

Measurements. Holotype female, length 2.7 mm, pleotelson width 0.6 mm.

Type locality. Misaki, Japan, collected by Dr. Th. Mortensen, May 26, 1914, low tide level, washed from the alga *Corallina.* The type and only one specimen is in the collections of the Universitetets Zoologiske Museum, Kϕbenhavn, Denmark.

Geographical distribution. Known only from the type locality.

Remarks. The structure of the mandibles and maxillipeds and the microscopic features of the pleotelson suggest that this species is closely related to *L. (P.) segnis.*

Limnoria (Phycolimnoria) nonsegnis, new species
Figure 39

Diagnosis. Flagellum of second antenna with three-four articles. Maxillipedal epipod strap-like, four times as long as wide, reaching the articulation of palp with endopod. Mandibular palp with three articles. Fifth somite of pleon with a mid-dorsal carina. Pleotelson with a mid-dorsal anteriorly located swelling followed by a pair of parallel carinae. Posterior edge of pleotelson with a fringe of dorsally directed spike-like setae but lacks tubercles. Lacinioid setae, two in number, are similar to the other setae of the setal row.

Measurements. Holotype male, length 3.0 mm, width of pleotelson 0.8 mm. Allotype, ovigerous, length 4.0 mm, width of pleotelson 1.0 mm.

Type locality. Port Arthur, Tasmania, holotype, allotype, and eleven female paratypes, from holdfast of *Macrocystis,* collected June 1951 by A. B. Cribb and sent to me by Frank McNeill, Curator of Invertebrates, at the Australian Museum, College Street, Sydney. The types have been returned to Frank McNeill.

Geographical distribution. Known only from the type locality.

Remarks. The ornamentation of the pleon and pleotelson resembles that of *L. (P.) segnis* considerably. It can be distinguished from *L. (P.) segnis* by its triarticulate mandibular palp and relatively short maxillipedal epipod.

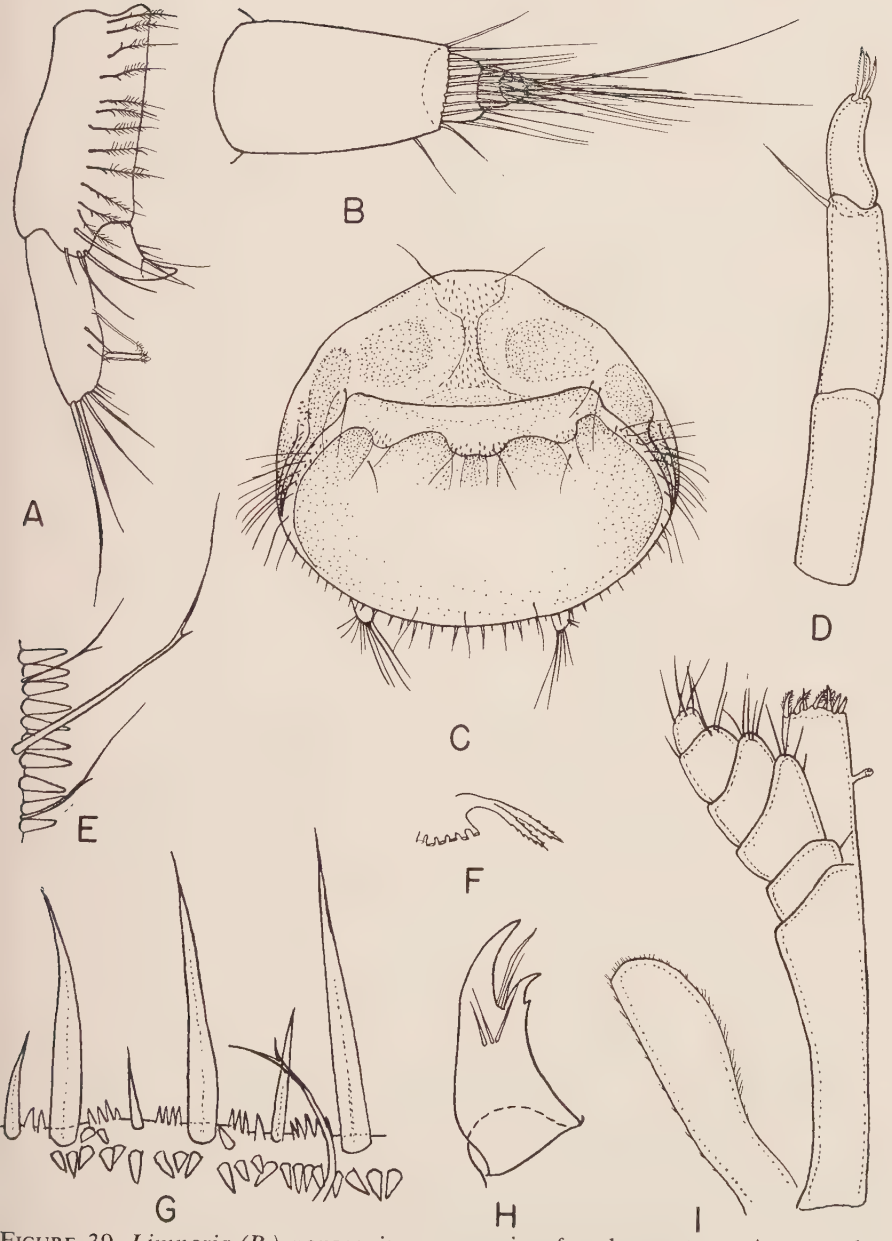

FIGURE 39. *Limnoria (P.) nonsegnis,* new species, female paratype. A, uropod. B, flagellum of second antenna. C, pleotelson. D, mandibular palp. E, lateral crest of pleotelson. F, setal row and lacinioid setae of right mandible. G, posterior margin of pleotelson. H, dactyl of first peraeopod. I, maxilliped. Figures with similar magnification, A, I; B, D, E, G, H; C; F (not known).

FIGURE 40. *Limnoria (P.) rugosissima,* new species, male paratype. A. distal article of first peraeopod. B, uropod. C, maxilliped. D, flagellum of second antenna. E, pleotelson. F, seta of penultimate article of mandibular palp. G, lacinioid seta of right mandible. H, right mandible inner surface. I, distal articles of first antenna. J, distal margin of pleotelson. K, lateral crest of pleotelson. Figures with similar magnification, A, D, H, I, J, K; B, C; E; F, G.

Limnoria (Phycolimnoria) rugosissima, new species
Figure 40

Diagnosis. Flagellum of first antenna with five articles. Epipod of maxilliped reaching only slightly beyond one-half the distance to the articulation of palp with endopod; epipod strap-like but with an acute distal end, being three and one-half times as long a wide. Mandibular palp with three articles. Fifth somite of pleon with large rugosities, pits, and ridges, irregular in pattern. Pleotelson with a pair of medial and lateral carinae; posterior margin with a fringe of dorsally directed spike-like setae near margin. Lacinioid seta of right mandible with an apical cluster of short, sharp denticles.

Measurements. Holotype, male, length 2.0 mm; width of pleotelson 0.5 mm. Allotype, length 2.0 mm, width of pleotelson 0.5 mm.

Type locality. The types, consisting of 14 specimens, were collected from Port Jackson, New South Wales, Australia. Twelve specimens were lent by Dr. E. Percival, Canterbury University College, Christchurch, New Zealand from the Chilton collection. Two paratypes also from the same collection were lent by Dr. Isabella Gordon, British Museum (Natural History). The specimens have been returned to Dr. Percival and Dr. Gordon.

Habitat. Although Chilton had identified the specimens as *Limnoria pfefferi* Stebbing, a wood-borer, the structure of the mandibles and the contents of the gut indicate this species is an algal borer.

Geographical distribution. Known only from the type locality.

Remarks. The rugose nature of the pleon and pleotelson, the pentarticulate second antennal flagellum, the triarticulate mandibular palp and the short maxillipedal epipod are features which distinguish this species from the other algal-boring species. Of the known species this one resembles *L. (P.) nonsegnis* most but is easily distinguished from it by the rugose pleotelson and short maxillipedal epipod.

Limnoria (Phycolimnoria) stephenseni, new species
Figures 41-42

Synonymy:

Limnoria antarctica Pfeffer. — Chilton, 1914a, pp. 382, 387 pl. XVII. — Hale, 1937, pp. 21-23, fig. 6. *Limnoria (pfefferi* Stebbing?), — Stephensen, 1927, pp. 361-362.

Diagnosis. Flagellum of second antenna with four articles. Epipod of maxilliped strap-like, about five times as long as wide and reaching beyond the articulation of palp with endopod. Mandibular palp with three articles. Fifth somite of pleon and pleotelson lacking ornamentation. Posterior margin of pleotelson with occasional large setae between which are small spike-like setae. Lacinioid seta of right mandible similar to the other setae in the setal row.

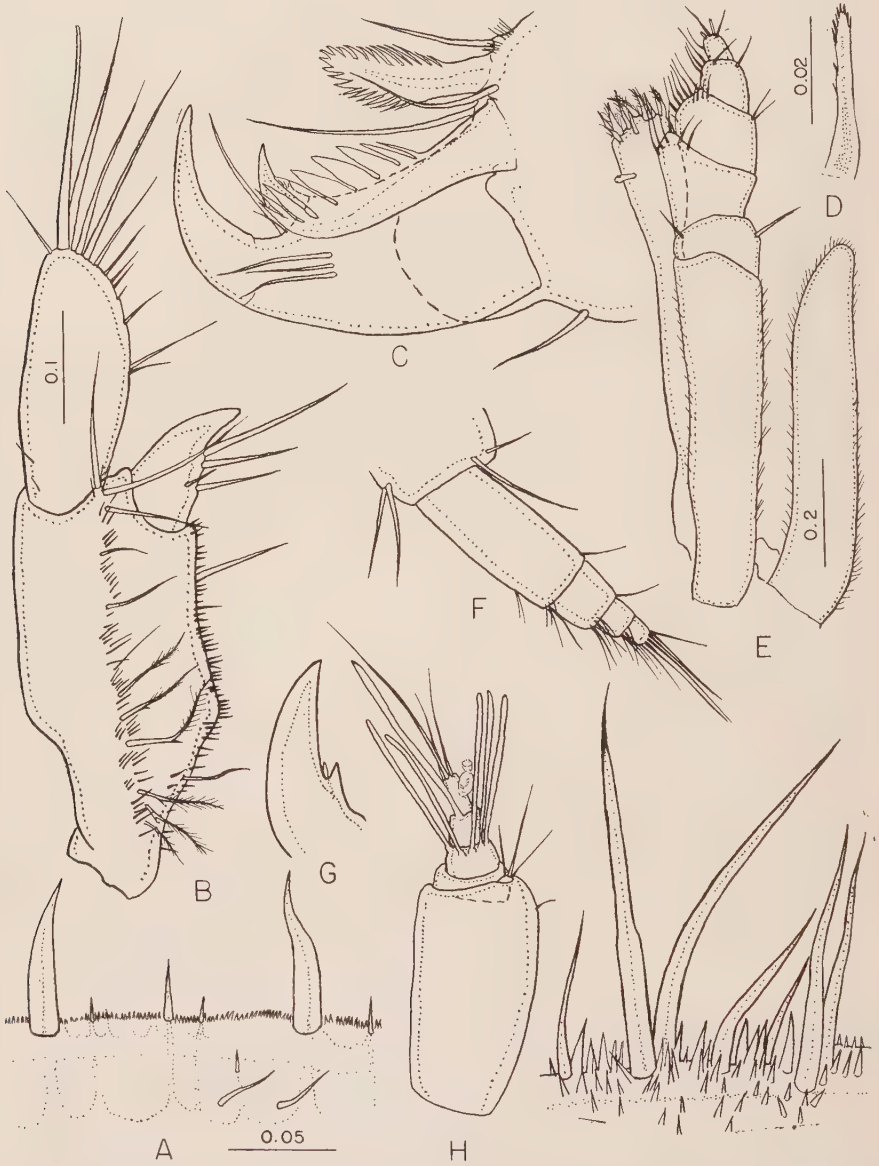

FIGURE 41. *Limnoria (P.) stephenseni*, new species, female. A, distal margin of pleotelson. B, uropod. C, distal parts of first peraeopod. D, lacinioid seta of right mandible. E, maxilliped. F, flagellum of second antenna. G, accessory claw, first peraeopod. H, distal articles of first antenna, note epizootic protozoan. I, lateral crest of pleotelson. Figures with similar magnification, A, C, H; B, F, G; D; E.

Measurements. One large female type was 8.0 mm in length and 2.6 mm in the width of the pleotelson.

Type locality. Auckland Islands, 33 type specimens, collected on Dr. Th. Mortensen's Pacific Expedition, 1914-1916. The specimens are in the collections of the Universitetets Zoologiske Museum, Copenhagen.

Geographical distribution. Auckland Isl., (Stephensen, 1927), *South Orkney* and *Macquarie Isls.* (Chilton, 1914a), *Macquarie Isls.* (Hale, 1937).

Remarks. Chilton (1914a) and Hale (1937) identified this species with *L. antarctica* Pfeffer but their figures show that this specimen had uropods more similar to those of *L. (P.) stephenseni.* Stephensen (1927) doubtfully referred the specimens to *L. (L.) pfefferi* Stebbing, a wood-borer, which however is large in size and similar to *L. (P.) stephenseni* in this respect. This species is the largest of all known species of *Limnoria* and is readily distinguished from the other algal-borers by the lack of ornamentation on its pleon and pleotelson. Hale's (1937) specimens were "found in burrows in roots of kelp—*Macrocystis.*"

Taxonomic Monstrosities, Nomina Nuda, and Invalid Species

Limnoria, like many other genera of the animal kingdom, has its share of unrecognizable species, nomina nuda, and animals incorrectly

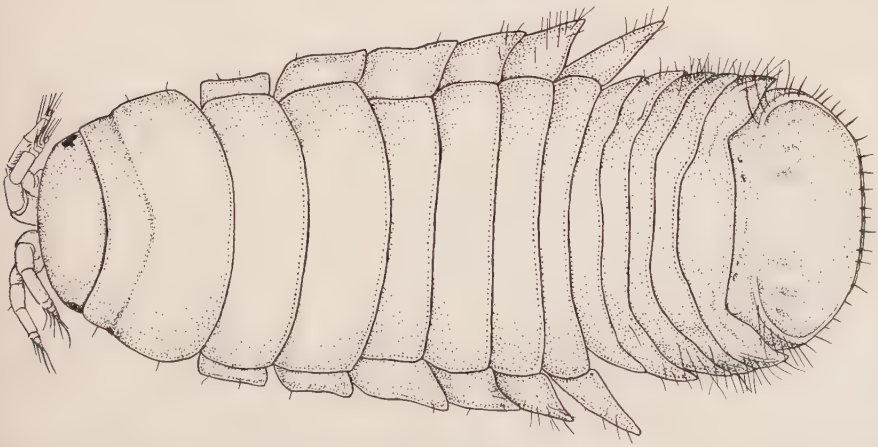

Figure 42. *Limnoria (P.) stephenseni,* new species, female slightly compressed, pleotelson foreshortened slightly, length of female 7.5 mm.

placed in the genus. Most writers have preferred to consider these as synonyms of *Limnoria lignorum* (Rathke). This treatment seems incorrect both biologically and taxonomically in every instance. Nomina nuda, names of animals lacking a description, are obviously not referable to any species until a description appears. It is equally inadvisable to consider names of animals which are not *Limnoria* as synonyms of *Limnoria*. For taxonomic and historical reasons it appears desirable that such troublesome forms be listed and discussed separately so that they may cause no further confusion with the valid forms of *Limnoria*.

1. *Limnoria Californica* Hewston, 1874, p. 24, *nomen nudum*.

In a report to the California Academy of Sciences, Dr. Hewston noted his find of a new species of *Limnoria* from San Francisco. This he provisionally called *Limnoria Californica*. No description ever appeared. Kofoid and Miller (1927, p. 309) considered this "species" to be undoubtedly *L. lignorum*." That this disposition of Hewston's name was incorrect is indicated by the fact that to date two species are known from San Francisco Bay (Menzies, Part I), neither of which is *L. lignorum*.

2. *Limnoria xylophaga* Hesse, 1868, pp. 101-120, pl. 9, figs. 1-37—Gerstaecker, 1882, p. 178.—Harger, 1880, p. 371.

This species is clearly an amphipod of the genus *Chelura*. Students of the Amphipoda have considered it a synonym of *Chelura terebrans* Philippi, 1839.

3. *Limnoria uncinata* Heller, 1886, pp. 734-735.—Carus, 1885, p. 451.—Gerstaecker, 1882, p. 178;—1883, p. 255.—Stalio, 1877, pp. 1367-1382.—Stossich, 1880, p. 228.

None of the writers subsequent to Heller added to his description or recognized his species. Most merely copied Heller's work or simply cited his paper. Harger (1880) considered this species a synonym of *Limnoria lignorum* (Rathke). Others have followed Harger's decision. Heller's species was collected "zu Verbosea auf der Insel Lesina" in the Adriatic. I have seen two species from the Adriatic *L. (L.) quadripunctata* Holthuis and *L. (L.) tripunctata* Menzies. Only one species, *L. terebrans* Leach, a synonym of *L. (L.) lignorum* was known to Heller. He distinguished between the two in the form of the uropods, being under the impression that the rami of those of *L. terebrans* were multiarticulate. His description of the uropods of *L. uncinata* corresponds generally with the structure

of those of all known species of *Limnoria*. Coldstream (1836, p. 321) described the uropodal rami of *L. terebrans* as multiarticulate and it is his error that lead Heller to believe that he had a new species. Indeed he probably did have one different from *L. lignorum* (=*L. terebrans*), but he in no way distinguished his species from *L. terebrans* (of Leach, not Coldstream). Had Heller been aware of Coldstream's error it is very doubtful that he would have described *L. uncinata*. There seems no real point in making either *L. (L.) quadripunctata* Holthuis or *L. (L.) tripunctata* Menzies, both of which are adequately described, synonyms of *uncinata* and reviving a name which has not been used since 1880.

4. *Limnoria gibbosa* Risso, Arcangeli, 1924, p. 7 (Carus, p. 451, ? Limnoria gibbosa Risso).

This species was assigned with doubt to *Limnoria* by Carus (1885, p. 451). Gourret (1891, p. 21-22) considered it a species of *Cymothoa*. Several of Risso's statements indicate that it does not belong to *Limnoria*. He states that the head is triangulate, which is not the case in *Limnoria* and, further, that "ses sept premiers segments sent ingaux," which is entirely unlike *Limnoria*.

A List of the Known Species of Limnoriidae

Present designation, original designation, most recent revision.

Wood-borers, *Limnoria (Limnoria)*

1. *lignorum* (Rathke), *Cymothoa lignorum* Rathke, 1799, this paper ..... p. 123
2. *pfefferi* Stebbing, *Limnoria pfefferi* Stebbing, 1905, this paper ..... p. 135
3. *japonica* Richardson, *Limnoria japonica* Richardson, 1909, this paper ..... p. 165
4. *septima* Barnard, *Limnoria septima* Barnard, 1936, this paper ..... p. 168
5. *quadripunctata* Holthuis, *Limnoria quadripunctata* Holthuis, 1949, this paper ..... p. 127
6. *tripunctata* Menzies, *Limnoria tripunctata* Menzies, 1951, this paper ..... p. 137
7. *platycauda* Menzies, *L. (L.) platycauda* Menzies, this paper ..... p. 139
8. *saseboensis* Menzies, *L. (L.) saseboensis* Menzies, this paper ..... p. 141

9. *simulata* Menzies, *L.* (*L.*) *simulata* Menzies, this paper . p. 144
10. *multipunctata* n. sp. . . . . p. 170
11. *unicornis* n. sp. . . . . p. 173
12. *foveolata* n. sp. . . . . p. 175
13. *sublittorale* n. sp. . . . . p. 175
14. *insulae* n. sp. . . . . p. 178

Seaweed-borers, *Limnoria (Phycolimnoria)*

15. *segnis* (Chilton), *Limnoria segnis* Chilton, 1883, this paper . . . . . p. 182
16. *antarctica* (Pfeffer), *Limnoria antarctica* Pfeffer, 1887, this paper . . . . . p. 180
17. *algarum* Menzies, *L.* (*P.*) *algarum* Menzies, this paper . . p. 146
18. *segnoides* n. sp. . . . . p. 184
19. *nonsegnis* n. sp. . . . . p. 186
20. *rugosissma* n. sp. . . . . p. 189
21. *stephenseni* n. sp. . . . . p. 189

Wood-borers, *Paralimnoria*

22. *andrewsi* (Calman), *Limnoria andrewsi* Calman, 1910, Menzies, this paper . . . . . p. 148

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